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The Eyes of the Blind Vertebrates of North America.

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I.

The Eyes of the Amblyopsidae.

By

C. H. Eigenmann.

With plates XI—XV and 10 Figures in text.

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The Eyes of the Blind Vertebrates of North America. I[1].

The Eyes of the Amblyopsidae[2].

By

Carl H. Eigenmann.

With Plates XI—XV and 10 Figures in text.

Eingegangen am 27. März 1899.

Introductory.

I propose to describe the eyes of the blind vertebrates of North America. The present paper is the first instalment of this work. It contains an account of the eyes of all the known species of the Amblyopsidae. As an introduction certain features of the eye of Zygonectes notatus, R., a member of a related family are given.

The Amblyopsidae offer exceptional facilities for the study of the steps in the degeneration of eyes. There are at least six species and we have gradations in habits from permanent epigean species to species that have for ages been established in caves.

1. Chologaster cornutus, Agassiz is abundant in the lowland streams and swamps in the South Atlantic states from Virginia to Florida. Maximum length about 55 mm.

2. Chologaster agassizii, Putnam is found in the underground streams of Kentucky and Tennessee. It is rare. Maximum length 62 mm.

3. Chologaster papilliferus, Forbes is found under stones in the springs of Southwestern Illinois, in Union and Jackson counties. Maximum length 55 mm.

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[1] The series of studies on the blind vertebrates of North America is gratefully inscribed on the completion of his twenty-fifth year as a teacher of zoology to David Starr Jordan, who has been to many, the writer included, a teacher, friend, and ever present inspiration.

[2] No. 23 of the contributions from the Zoological Laboratory of the Indiana University.

4. Amblyopsis spelæus, DeKay is found widely distributed in the caves east of the Mississippi both north and south of the Ohio river. Maximum length 135 mm.

5. Typhlichthys subterraneus, Girard is found with the latter species in the caves east of the Mississippi, but is confined chiefly if not altogether to the south side of the Ohio river. But a single specimen of Typhlichthys has been found north of the Ohio and it is probably specifically distinct from T. subterraneus. Maximum length 55 mm.

6. Troglichthys rosae, Eigenmann is found in the caves west of the Mississippi river. Maximum length 55 mm.

The first two species mentioned live, as far as known, altogether in epigean streams; the others altogether in subterranean streams.

Chologaster possesses well developed eyes, the others mere vestiges. We have thus two epigean species with well developed eyes, one subterranean species with well developed eyes and three subterranean species with greatly degenerate eyes. The three latter species are descended from three distinct epigean ancestors. Amblyopsis is the only member of the family possessing ventral fins, and Troglichthys possesses scleral cartilages which are not found in the other members excepting Amblyopsis.

It must be apparent that an experiment on a vast scale has been conducted by nature, leaving us but to read the results. Moreover the experiment is one in evolution without the assistance or intervention of natural selection.

The Trustees of the Elizabeth Thompson Science fund granted me $ 100.00. The material on which the account of the eye of Chologaster agassizii, P. and Troglichthys rosae, E. are based was collected with this fund, as well as the material for the embryology of Amblyopsis which will be dealt with in another paper.

I wish to thank the officials of the Monon, L. E. & St. L., L. & N. and Frisco Railways for transportation over their lines. Without the coöperation of the Rail Roads it would have been impossible for me to bring together the widely scattered species of the North American Blind fishes. I am especially indebted to Mr. H. C. Ganter, the manager of the Mammoth Cave, for the privilege of collecting in the cave, for guides and many other favors. Further I am indebted to Mr. E. B. Forbes for securing me 30 living Chologaster papilliferus; to Mr. George Harris of Cassville, Mo., and various other gentlemen in Indiana and Missouri for personal assistance.

Mr. S. Garman presented me with two specimens of Troglichthys,

and the National Museum sent me a series of the Amblyopsidae for examination. Prof. D. W. Dennis made a series of microphotographs.

Mrs. Adelaide Newsom and my colleague Mr. Alfred Mansfield Brooks made color sketches of Amblyopsis for me.

I. Special Part.

The eyes of a number of species of fishes in addition to those of the Amblyopsidae were examined, viz. those of Cymatogaster aggregatus, G., Typhlogobius californiensis, St., Carassius auratus, L., Ameiurus sp., Coregonus sp. and Zygonectes notatus, Raf. I shall briefly describe the eyes of but one of these.

The topographical relationships of the cells of the retina obtained an entirely new light by the application of the Methylen blue method chiefly on the part of Dogiel, and the Golgi method principally through Ramón y Cajal. The latter has treated the retina of fishes more particularly.

The layers of the retina of fishes as made out by Ramón y Cajal '95 are as follows; beginning at the periphery and going toward the center of the eye:

1. Epithelial-pigment layer.
2. Rods and cones.
3. Outer nuclear layer.
4. Outer molecular layer.
5. Horizontal cells.
6. Bipolar cells.
7. Spongioblasts.
8. Inner molecular layer.
9. Ganglionic layer.
10. Optic fiber layer.

The layers will be designated on the figures and frequently in the texts by these numbers. The literature bearing on this group of fish eyes will be given under the different species. But one paper has appeared since the introduction of the microtome.

1. The eyes of Zygonectes. (Figs. 10 and 11.)

Zygonectes notatus was selected for comparison because it is a member of the Cyprinodontidae, a family closely related to the Amblyopsidae. I am not aware that this species has any advantage over other species of the family. It has large, well developed eyes, that we may assume to be fully and normally developed. The material examined was alcoholic. It had been preserved by simply placing in alcohol without any intention of future histological examination, but the structures were all well preserved for topographic relations. The protoplasmic and nervous processes of the cells were of course not brought out as with GOLGI's method.

In a specimen 38 mm long the eye measures 2.24 mm in length, 2 mm in vertical diameter, 1.12 mm from the axis of the optic nerve to the front of the iris, 1.6 mm from the axis of the optic nerve to the front of the cornea. The lens measures 0.96 mm in diameter.

The pigment layer measures	56 μ
Outer nuclear layer	36 -
Outer reticular.	4 -
Tangential cell layer . . .	9 -
Inner nuclear	40 -
Inner reticular	52 -
Ganglionic layer	12 -
Optic fiber layer.	28 -
Total thickness of retina .	237 μ

The regularity of arrangement of rods and cones is very striking. The basal portion of the rods contains refractive granules increasing in size outward where the series ends in a lenticular vacuolated body separating the granular from the distal portion of the rod. The cones are all twins without any granulation. This marked difference between the two enables one to distinguish in tangential sections between them at a glance. The twin cones are arranged in series in such a manner that the axes joining the cones in any neighboring series are at right angles to each other, while in every alternate series they extend in approximately the same or parallel directions. The rods alternate in all directions with twin cones[1]). Fig. 10.

The outer nuclei are irregular, compressed and elongate, forming two distinct layers. The outer molecular layer has an irregular outer boundary produced by the process extending towards the outer cells. The inner nuclear layer is divided into an outer layer of small bipolar cells and an inner layer of larger, more coarsely granulated spongioblastic cells. When any breaks occur in the retina, owing to mechanical or chemical causes, the breaks usually occur between these outer bipolar and inner spongiose cells of the inner nuclear layer.

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[1]) This condition described by RYDER for young trout has been found by Mr. G. HANSEL and myself in a large series of fishes. The matter will be treated at another place. There may be a question whether the simple elements considered as rods are not single cones. MÜLLER '72 page 59 speaking of Perca says »each single cone is separated from its neighbor by twins, not counting the rods«.

2. The eyes of Chologaster papilliferus, Forbes. (Figs. 12—20.)

The only account of the eyes of Chologaster, aside from the measurements in the description of the species, is a note by Wright, '85. Professor Wright obtained his specimen from Professor S. A. Forbes and had therefore C. papilliferus. He announced that the pigment is absent in the pigmentary layer of the retina of this species. But this condition was unquestionably either accidental or due to the reagents employed. Chromic acid partly or wholly removes the pigment, leaving the cells in good condition.

The vertical diameter of the eye in a specimen 39 mm long is 640 μ; in a specimen 55 mm long (the largest secured) 960 μ. The distance from the point of entrance of the optic nerve to the front of the cornea 560 μ and 900 μ respectively in the two specimens. The distance from the point of entrance of the optic nerve to the front of the epidermis over the eye is 600 μ in the smaller specimens, the lens about 360 μ in diameter. For further measurements see the table page 558.

The eye is small when compared with that of other fishes of the same size, and especially so when compared with the eyes of the Zygonectes. It is located high up on the side of the head, its upper surface being nearly on a level with the top of the head. It is directed outward and forward. In a specimen 35 mm long it is 1.44 mm from the tip of the snout 0.88 mm long. The distance between the eyes 1.60 mm.

The dermis over the eye is thinner than elsewhere and devoid of pigment. The epidermis passes directly over the eye without any free orbital rim. It is much thinner, 24 μ in specimen 39 mm long, than elsewhere about the side of the head (50—60 μ) and consists solely of epithelial cells which are columnar at the base and flat horizontal at the free end of the epidermis. All the other elements of the epidermis, goblet cells, mucous cells, very abundant all about the eye, are totally absent over it (Cut 1).

The six normal eye muscles are present in Chologaster. The four rectus muscles arise near a common point just behind the point of exit of the optic nerve from the skull. The M. rectus superior passes from this point outward, upward and forward. The M. rectus inferior passes nearly horizontally outward and forward. The M. rectus externus passes nearly straight out at right angles to the axis of the body to the posterior face of the bulb. The M. r. internus is probably the longest, passing outward and forward to the anterior face of the eye.

The two oblique muscles originate near a common point well in front of the exit of the optic nerve and are inserted near the insertion of the M. rectus superior and inferior. There is nothing remarkable about any of these muscles and they are mentioned solely as a basis of comparison with the condition found in Amblyopsis. The space from the wall of the brain case outward about the eye muscles and eye is bounded by a connective tissue capsule. Within this capsule, the space between the muscles and the posterior part of the optic pit and the eye is filled with fat. Above this capsule lies another mass of fat and below it still another (Cut 2).

The supra orbital does not help to protect the eye which lies entirely lateral from it and extends above it. The suborbital bones are thin hollowed sheets of bone just back of the suborbital mucous canal. Their number etc. has not been determined, but their location is of importance in view of a statement made by Kohl concerning their absence in Troglichthys.

The sclera is represented by a thin fibrous capsule which is sometimes widely separated from the eye by reagents. In the largest specimen it is but 4 μ thick. It is continued over the front of the eye in contact with the dermis as a thin cornea (see Cut 1). This is much more compact than the rest of the sclera. It readily separates from the dermis. The sclera is never at any place cartilagenous. I was at some trouble to demonstrate the absence of cartilage even in the largest specimen in order to detect if possible the homologues of the cartilages in Amblyopsis and Troglichthys rosae and can state positively that no cartilage is found associated with the eye of Chologaster papilliferus or in fact with the eye of any of the species of Chologaster.

The choroid is very thin. Just within the sclera is a homogeneous, sometimes excessively thin, layer containing a few nuclei, the Suprachoroidal Lymphspace. If the eye contracts through reagents the choroid which clings to the eye ball is separated from the sclera by the widening of this space. Pigment is not abundant except over the iris and below and at the sides of the entrance of the optic nerve. About the entrance of the optic nerve a mass of pigment is prominent being especially conspicuous in the largest specimen (Cut 3). A mass of pigment which may be homologous with this has been described by Ritter in Typhlogobius. Ritter page 62 found no cellular structure in the pigmented mass in Typhlogobius and he identified this pigmented mass as the choroid gland. A choroid gland or the rete mirabile is not found. A Processus falciformis is not present. Blood vessels are not numerous and a distinct vascular layer of the choroid I have not been able to separate. In the largest specimen the choroid is much richer in blood vessels ventral of the pigmented mass at the entrance of the optic nerve than elsewhere. The capillary layer reaches here a total of 9 μ in thickness. A layer of excessively thin pigment cells lies close to the pigmented layer of the retina. It is so thin and so closely applied to the pigmented layer of the retina that it is only in a few tangential sections that this part of the choroid becomes evident.

The optic nerve enters the retina as a single strand. It spreads out in all directions as soon as it has passed the pigmented portion of the retina (see Cut 3). Some of the fibers pass behind the ganglionic cells just within the entrance of the optic nerve, a condition of importance in the interpretation of the distribution of the optic nerve in the blind members of the family. The diameter of the n. opticus at the entrance into the pigment layer is 32 μ in the largest specimen. The nerve is not spread out over the ganglionic layer, but is distributed in well defined tracts between the nuclei. There is no nerve fiber layer proper (Fig. 12 and Cut 3). These strands of fiber not only entirely displace the ganglionic cells along their track, but also plow into the granular layer.

The pigment layer of the retina is very thick, as compared with the other layers, a condition recalling that described by Ritter for Typhlogobius and usually to be found in degenerate eyes.

For a comparative statement of the thickness of the various layers of the retina see Table on page 558.

The pigmentary layer is half the total thickness of the retina in the smaller specimen, while in the largest it is still thicker, measuring 104 of the 168 μ of the retinal thickness.

About $^1/_8$ of the outer part of this layer usually appears as a solid mass of pigment where the margins of the cells touch, just within this is a region where the cells are contracted, there being large open pigmentless spaces; at the innermost part there is again an accumulation of granular or rod shaped pigment granules which obscure almost everything else in the ordinary sections (see Cut 3). Specimens preserved in chromic acid lose most or all of their pigment which becomes brownish or disappears. The nuclei of the pigment cells are very irregular in outline (Fig. 14) appearing to have no more definite shape than those of white blood corpuscles. Hollow processes extend from the cell body downward to near the external limiting membrane (Figs. 13, 14).

About the bodies of the cones the pigment is in thin strands of which there are 8 to 12 to each twin cone: farther out it forms a complete ring about them. The cones are twins, rarely three are associated together. The twins are nearly all arranged in such a manner that the line, which may be termed the axis, connecting the centers of the components of a twin are nearly parallel and form approximately part of an equatorial circumference of the eye (Fig. 16 *C*). There is therefore no resemblance to the condition found in Coregonus and Zygonectes even if we omit for the present the consideration of the rods (or single cones). The cones consist of an outer segment (80 μ long in the largest specimen) with a tendency to become oblique near their outer ends. In chromic preparations these readily split into discs. They stain faintly but evenly. They are joined by a translucent interval to the body of the cone, an ellipsoid body 5 μ + 10 μ taking on a deep stain (Fig. 15, 2). These rest apparently on a membrane cylinder extending from their base to near the external limiting membrane, a distance of 10 μ. Here they rest on a deeply staining cone-shaped cell body which pierces the external limiting membrane and is extended as a less deeply staining, nodulated process to the outer reticular layer where it spreads out into a cone-shaped base.

The rods are very much fewer in number and not regularly arranged. They are much fewer than the number of nuclei in the outer nuclear layer exclusive of the cone nuclei. But extending just without the external limiting membrane a large number of short processes are seen between the cone nuclei Fig. 16. Whether these are degenerate rods I am unable to say.

The outer nuclear layer differs materially in the younger, i. e. smaller (29 mm) specimens and in the largest specimens. In the younger specimens it consists of several (2—3) layers of cells exclusive of the cone cells, which in this case can be counted with the layer of rods and cones. In the larger specimens this is reduced to a single layer of nuclei less densely packed, with occasionally a horizontal nucleus near the base which is less granular, staining a more uniform color.

In the largest specimen the outer nuclear layer makes up about 7% of the total thickness of the retina, in the smaller specimens it is slightly thicker forming 10% of the total thickness.

The outer granular layer differs also materially in the largest and smallest specimens. In the largest it forms a thin layer entirely free from nuclei and with a total thickness of but 2 or 3 μ.

In a specimen 39 mm long this layer is 5 μ thick, distinctly granular, contains a few round nuclei — not differing from those of the inner nuclear layer. (See Cut 3.) These are probably members of the layer of fulcrum cells. The latter are not separable from the underlying bipolar cells in other regions. In tangential sections they appear in groups of two, but are much fewer in number than the twin cone cell Fig. 16. The inner layer of the inner nuclear layer is composed of distinctly larger cells in the largest specimen and separated from the rest by a slight interval. The cells here form a distinct row in section, while the rest for the most part are irregularly placed. The difference in size is especially noticeable near the entrance of the optic nerve. The nuclei are mostly spherical. A few nuclei are found more elongate and with their longer axis at right angles to the retina (Müller's fiber nuclei). The largest spherical nuclei measure 5 μ in diameter. The inner granular layer varies in thickness and contains few cells.

The ganglionic layer consists of a single layer of nuclei, rather irregularly placed. The nuclei measure 6 μ in diameter. For reasons explained in a previous paragraph a distinct nerve fiber layer is not present. A thin nucleate membrane, the hyaloid membrane, containing the blood vessels, lies directly on the ganglionic layer. (Cut 3.)

It is quite evident from the foregoing that the retina is very much simplified as compared with that of Zygonectes. The point of greatest degeneration lies between the outer nuclear and inner reticular layers. The horizontal nuclei are all but entirely eliminated. The bipolar cells are, in the adult, reduced to two layers of nuclei, and the spongioblasts are reduced to a single layer of cells. Even this distinction and differentiation is only seen in the largest individuals. Twin cones are abundant and apparently not lacking in number and structure, but are arranged in a different manner. Rods are much fewer in number than in either Coregonus or Zygonectes.

The chief difference between the youngest and oldest specimens of papilliferus examined lies in the thickness of the pigmented layer and the outer nucleated and the outer granular layer. The relative thickness of the pigmented layer increases very much with age.

The irideal region needs a few words since its structure helps to explain certain conditions in the blind fishes. The epithelial part is composed of two layers of cubical cells of which the outer are the larger. The outer cells are normally filled with pigment to such an extent that their outlines can not be made out, the inner cells are free from pigment. The outer layer passes directly over into the pigmented layer of the retina. Where the inner layer of the iris merges into the inner layers of the retina it is composed of a group of cells with elongated nuclei (cut 4). The uveal part of the iris is composed of a thin layer of cells with irregular nuclei and the pigment cells of this layer are much thinner than the epithelial pigment. The ligamentum ciliary does not contain many muscle fibers, but is abundantly supplied with granular nuclei. The things of greatest importance are these granular nuclei, the epithelial pigment and the oval nuclei at the ora serata. As compared with the same region in other fishes the shortness of the section of the iris is at once striking, figures 10 and 10*a*. The absence of ciliary muscles and the insignificance of DECEMET's membrane are also notable.

The lens offers no peculiarities. The shape of its epithelial nuclei may be gathered from figure 20 and cut 5.

3. The eyes of Chologaster agassizii, Putnam.

As far as I know but a single specimen of this species has been put on record. PUTNAM described it from Lebanon, Tennessee. The present account is based on five specimens secured by me in the River Styx in Mammoth cave and in Cedar Sinks.

The eye of Chologaster agassizii is much smaller than that of Chologaster papilliferus. In a specimen 41 mm long it is placed 2.08 mm from the tip of the snout, the eye measuring 0.72 mm in diameter. The distance from eye to eye is 2.72 mm. It is elliptical in outline with the lateral face depressed. It is directed outward. The optic nerve, which, at its origin, is surrounded by pigment for a distance of 2.4 mm extends almost straight inward. The dermis over the eye is essentially as in papilliferus. The epidermis is less simplified. It is thinner than in the surrounding tissue, but goblet cells are found in it although they are much smaller and much less numerous than elsewhere. The sclera and choroid are as in papilliferus, including a pigment mass below the exit of the optic nerve just within the sclera. The optic nerve measures 24 μ at its point of entrance into the pigment layer of the retina and is thus one-fourth smaller in diameter than in papilliferus.

The proportionate thickness of the retinal layers as compared with the layers of C. papilliferus is seen in the table. The maximum thickness in the largest specimen is but 130 μ as compared with 166 μ in papilliferus. This difference is almost entirely due to the thickness of the pigment layer, which is 74 μ in the largest agassizii, and 104 μ in the largest papilliferus, leaving a difference of but 6 μ in the other layers. The pigmented layer is, on an average, much thinner than in papilliferus. Yet the percent. of the total thickness of the retina in pigment is larger than in normal fishes. The nuclei of the pigmented epithelium are irregular in outline. The part of the pigment layer about the nuclei forms a mass of pigment in which cell boundaries cannot always be made out. The pigment about the nucleus is in granules; further in about the cone bodies it is in prisms. I have not been able to make out rods. The cones are irregularly elongate so that the cone bodies are at various hights. The pattern of the twin cones has, therefore, not been made out.

The outer nuclear layer consists of nuclei conical in shape and partly without the outer limiting membrane as in papilliferus, and a number of oval nuclei forming a double series within these in the younger, a single series in the older specimens.

The outer reticular layer is distinct to the iris. Horizontal cells could not, with certainty, be identified. Some cells lie without the inner nuclear layer in the outer reticular layer and may be fulcrum cells. The inner nuclear layer is three to four series of cells deep. Müllerian nuclei are present. If artificial splitting take place the innermost series of nuclei separates from the outer layers; these probably correspond to the spongiblast cells of other retinas. The inner reticular layer is well defined and contains very few cells. The ganglionic layer consists of a single series of nuclei. A distinct optic fibre layer is not present.

The iris is much as in C. papilliferus, much shorter in section than in C. cornutus. The inner cells of the retinal portion are pigmented around the margins of the pupil, while in papilliferus only the outer cells carry pigment.

4. The Eyes of Chologaster cornutus, Agassiz.

The eye of this species is much larger than that of the other species of the genus. The retina on the other hand is simpler. The details of the measurements are given at the end of the account of this eye.

I have had but two specimens for examination; they were preserved in alcohol and respectively 27 and 43 mm long. The very remarkable retina deserves much fuller treatment than is possible with the limited material available[1]. Leaving out of consideration the accessory structures of the eye as choroid, sclera, muscles etc. which are scarcely if at all different from the same structures in papilliferus, the retinal characters may be briefly described.

The pigment layer is very thick as compared with the rest of the retina forming over 60% of the total thickness. The pigment cells form a sheath common to any pair of the twin cones.

Connections between the cones and the outer nuclei could not be made out. There are apparently fewer cones than nuclei. For the relation of the cones to the underlying cells and of the latter to the nuclei of the inner nuclear layer see figures 23 and 24.

The outer nuclear layer consists of a series of nuclei closely packed together with their longer axes vertical. Occasionally a fainter staining nucleus is found among the bases of these cells with its longer axis horizontal. Figures 21, 23, 26, 27.

The outer reticular layer is well developed. Its boundary is irregular on the side of the inner nuclear layer, but more regular on the side of the outer nuclear layer.

Horizontal cells are very few and widely separated, if, indeed this layer is represented at all. A few cells horizontally placed are present on the inner face of the outer reticular layer, figure 21.

The inner nuclear layer is represented in the smaller specimen by two series of small rounded nuclei, figure 21. In the larger specimen a single irregular series represents this layer, figures 26 and 27. Besides the rounded nuclei there are a few irregular shaped ones and other elongated ones. Some of the latter lie in the plane of this layer, others at right angles to it. The latter are probably Müllerian nuclei.

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[1] Numerous attempts through friends and through dealers to secure living material has failed. The U. S. Fish Commission has promised to make an effort in this direction and the present account may be looked upon as preliminary.

The inner reticular layer is well developed and contains a few round nuclei as in papilliferus. In addition it contains some vertically elongated nuclei at times reaching through half the thickness of the layer. These are also evidently Müllerian nuclei. Some of them extend from the ganglionic layer outward, others from the inner nuclear layer inward, figures 21, 26.

The ganglionic layer is very imperfect, being represented by scattered nuclei imbeded in the inner layer of the reticular layer. In this layer we have a decided degeneration by a reduction of the number of elements, figure 25.

A nerve fiber layer is not evident in cross section.

The pigmented layer has not been decreased nor have the reticular layers degenerated materially beyond Ch. papilliferus. The nuclear layers on the other hand have been very materially affected. The outer layer has been much reduced. But this need not necessarily imply degeneration. The inner nuclear layer has been reduced $^1/_3$ and more from the lowest point in papilliferus. There is no longer any definite difference between the inner spongiose and outer bipolar cells of this layer, a difference that is usually well marked and is still evident in papilliferus. An equally marked change has unquestionably occurred in the ganglionic layer where a layer of cells, continuous but for the strands of the n. opticus passing between them, has dwindled to irregularly scattered cells.

The position of the Müllerian fiber nuclei are also unique in this retina.

The eye is in some respects more degenerate than that of Typhlichthys subterraneus. The dioptric arrangements in this eye and the cones are better developed and the layers in general are better differentiated than in T. subterraneus, but the nuclear layers are in the latter species composed of more series of cells.

A section of the iris is much longer than in either of the other species of this genus.

Since the differences in the eye and retina of the species of Chologaster are largely a matter of measurements I add the following tables.

Measurements of the Eyes of Chologaster in groups.

Treated alike.

	Vertical diam.	Longitud. diam.	Medio lateral diam. with the lens	Pupil	Lens
a) Eye dissected out and measured directly:					
Cholog. cornutus, Agassiz, 32 mm long	960 µ	1120 µ	752 µ	—	544 µ
45 mm -	1200 µ	1360 µ	688 µ	—	—
Cholog. papilliferus, Forbes, 32 mm long	832 µ	888 µ	816 µ (720 without lens)	320 µ	390 µ
Cholog. agassizii, Putnam, 39 mm long	720 µ	800 µ	560 µ	304 µ	336 µ
b) Head mounted in balsam, the eyes measured from above:			Medio lateral without the lens		
Cholog. papilliferus, Forbes, 35 mm long.	—	880 µ	640 µ (612 without lens) (688 with cornea)	—	—
Cholog. agassizii, Putnam, 41 mm long.	—	720 µ	486 µ (576 with cornea)	—	—
c) Heads sectioned in paraffine:			Medio lateral		
Cholog. cornutus, Agassiz, 27 mm long.	720-800 µ	—	672 µ	—	480 µ
Cholog. papilliferus, Forbes, 39 mm long.	640 µ	805 µ	560 µ with cornea	—	360 µ
Cholog. agassizii, Putnam, 38 mm long.	536 µ	738 µ about	520 µ with cornea	—	296 µ

Measurements of the retina of species of Chologaster.

Only the averages of from two to nine measurements are given in each case.

	Cornutus		Papilliferus		Agassizii	
	27 mm	43 mm	29-39 mm	55 mm	38 mm	62 mm
Pigment	47 µ	52½	64½	102	48½	74
Outer nuclear . . .	4	4½	13½	13	14	10
Outer reticular . .	2	1½	3	2	2	3
Inner nuclear . . .	6	7½	18	19½	20	22
Inner reticular . .	9	13	15	17	14½	16
Ganglionic	5	4½	8	9	8	5
	73	83½	122	162½	107	130

From this table it will be seen that the retina of agassizii differs from that of papilliferus almost altogether in the decrease of the thickness of the pigment epithelium. The retina of cornutus differs from that of agassizii in the reduction of the layers inside of the pigment epithelium.

5. The Eyes of Amblyopsis spelæus, De Kay.

The eyes of Amblyopsis have been described by Tellkampf, Wyman and Putnam. These authors gave general accounts of the eyes as far as this could be done without serial sections and their accounts are far from satisfactory. It is therefore unfortunate that Kohl, who had less material of a supposed Typhlichthys from Missouri, should have based a criticism of the facts observed by Wyman in Amblyopsis on what he saw especially since scarcely a statement made by Kohl corresponds to a condition found in Amblyopsis, or even the Typhlichthys subterraneus from Mammoth cave. An abstract of Kohl's result will be given under Troglichthys.

Tellkampf, '44, first pointed out the presence of rudimentary eyes and states that these can be seen in some specimens as black spots under the skin by means of a powerful lens. The statement that the eyes are externally visible in some specimens, afterwards thrown in doubt by Kohl, is perfectly correct. The eye of Amblyopsis can be seen as a black spot with the unaided eye in specimens up to 50 mm in length.

Wyman, in Putnam '71, figured the optic nerve, a lens and muscular bands attached to the exterior of the globe, but did not recognize them as homologues of the muscles of the normal eyes of fishes. In a four inch fish, Wyman '54, found the eye to be $^1/_{16}$ of an inch in its long diameter. A nerve filament was traced to the cranial wall, but further it could not be followed. The eye is made up of 1) a thin membrane, the sclera, 2) a layer of pigment cells, the choroid which were most abundant about the anterior part of the eye, 3) a single layer of colorless cells larger than the pigment cells, the retina, 4) just in front of the globe a lenticular-shaped, transparent body, the lens, 5) the whole surrounded by loose areolar tissue.

Wyman was mistaken in his identification of No. 2, 4, and part of 3.

Of this species I have had an unlimited supply of fresh material from the Donelson and Hamer caves in Lawrence County, Indiana. The details of the development of the eye will follow. I shall here give only the histology of the eyes of fishes from 25 mm long to their maximum size, 135 mm.

In well fed adult specimens of Amblyopsis there is no external indication of an eye. In poor individuals the large amount of fat surrounding the eye and collected in a ball-shaped mass becomes apparent through the translucent skin. In young specimens, before they have reached a length of 50 mm, the eyes are perfectly evident from the surface. By this I do not mean that they are conspicuous, for the minute eyes would not be conspicuous were they situated just beneath the skin. The skin is not modified in the region over the eyes, but has the same structure it possesses in the neighboring regions. This condition is in strong contrast to the conditions described for Chologaster papilliferus. The position of the eye can be determined from the surface in older individuals by certain tactile ridges, being between a long longitudinal ridge (supraorbital) situated caudad of the posterior nares and two vertical (suborbital) ridges. They can also be approximately located by the mucous canals, being situated above the middle of the suborbital canal forward from the fork of the suborbital and rostral canals. The exact location in relation to these ridges differs however to some extent in different specimens.

The skull is surprisingly little modified, there being deep orbital notches, large enough to accommodate a large eye. The maintenance of this skull structure long after the eye has dwindled is significant in the consideration of the causes of degeneration and will be referred to again.

The change in the relation of the eye to surrounding tissues as well as the relative size can best be gathered from the accompanying figures of cross-sections of Chologaster and of Amblyopsis drawn with the same magnification, but from different sized individuals (Cuts 6 and 7).

Beneath the dermis (black in the cuts) a thick layer of connective tissue has developed in Amblyopsis. The large fibrous capsule occupied by the eye, eye muscles and orbital fat in Chologaster has in Amblyopsis been largely filled with fat. There is no indication of fatty degeneration; it is simply the accumulation of fatty cells in the eye cavity. The eye is very small and lies on the floor of the optic capsule. The infraorbital and supraorbital fat masses described for Chologaster papilliferus are also large in Amblyopsis and form especially large masses in front and behind the optic capsule. In Chologaster the brain extends forward beyond the front of the eye, while in Amblyopsis the brain does not extend as far forward, the anterior portion of the brain cavity being filled with fat. Attention may also be called here to the presence and position of the suborbital bones which Kohl says are represented in Troglichthys by the cartilagenous masses forming a hood over the front of the eye.

These cartilages are present in front of the Amblyopsis eye and it can readily be seen that they have nothing to do with the suborbital bones.

The adult eye of Amblyopsis with its appurtenances may now be taken up seriatim.

The eye occupies the lower part of the eye cavity. It is surrounded by loose connective tissue which is so associated with the eye that if, through reagents, contractions occur, as frequently happens, a space is left between the eye with its connective tissue and the septum forming the lower floor of the eye cavity. Above the eye with its connective tissue is the large accumulation of fat mentioned above. From the eye to the inner wall of the orbit extends a continuation of the connective tissue surrounding the eye. In this continuation of the connective tissue the optic nerve and eye muscles extend. In the longest individual, 135 mm long, the eyes were removed 5 mm from the surface of the epidermis.

The shape of the eye together with the pigment variously scattered in the connective tissue associated with it is very variable, differing from sub-spherical in the smaller individuals to long spindle-shaped in the old. Considerable difference is found in the shape of the eye itself. See table of measurements page 570.

Pigment is found in very variable quantity and variously scattered in the connective tissue surrounding the eye. The amount of this pigment seems to vary inversely with the amount of pigment in the eye itself, and to increase with age.

As WYMAN has stated and figured, eye muscles are present in Amblyopsis, but, contrary to his statement, they are the homologues of the normal eye muscles. Not all preparations are equally good for tracing the muscles. They are best demonstrated in heads treated entire by GOLGI's method and sectioned in celloidin. While the muscles have been noted in a variety of preparations the description will be drawn from those treated by GOLGI's silver method and stained at times with Haemalum or BIONDI-EHRLICH's three color stain[1].

In one individual the upper rectus and upper oblique muscles are inserted together on the upper median surface of the eye, or more exactly on the upper posterior angle of the upper scleral cartilage. The lower oblique is inserted opposite this place. From these places the oblique muscles extend inward and forward. The origin of the lower oblique is 0.72 mm in front of its insertion, while of the larger upper oblique extends a little further forward, being inserted 0.85 mm behind its origin. It takes its origin in the projecting angle of a cartilage above and in advance of the origin of the lower oblique. In the inner part of the orbit a small muscle extends from the inferior oblique horizontally backward, taking its origin with the rectus muscles. This muscle in its posterior extent has the characteristics of the inner rectus. But whether or not its fibers reach the eye I was unable to determine. If they do they reach it with the fibers of the lower oblique.

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[1] GOLGI's method did not give the desired results for nervous structures, but by staining with the above methods the material was found excellent for general purposes.

The rectus muscles arise from the lateral margin of the bone forming the brain case just behind the anterior end of the brain, the upper rectus taking its origin behind the others. They extend as four bundles forward in a connective tissue tube. Before leaving this tube they are reduced to three bundles by the union of a small bundle situated above the others in the tube with the largest bundle situated nearest the outer margin. One of these is the lower rectus. The largest one is the upper rectus and the one joining it, in all probability, the external rectus. The external rectus, if I am correct in the identification, is not distinguishable from the latter during the rest of its course nor in its insertion in the sclera. The entrance of the rectus muscles into the connective tissue sheath occurs 0.5 mm behind their insertion in the eye. We have in this eye the two oblique muscles, the upper rectus, the lower rectus, a small bundle of fibers following for the most part the course of the upper rectus, the external rectus, and a small bundle of fibers extending from the origin of the rectus muscles forward to the lower oblique which may be the inner rectus. We have at least five, probably all six of the muscles normal to fish eyes. But that this is not always the case is very strikingly emphasised by the fact that the eye of the opposite side of the same individual lacks the upper oblique.

In another individual the superior rectus and superior oblique are the only muscles present on the left, while on the right the upper rectus is the only muscle present. The preparations of this individual are particularly favorable for tracing the muscles. They are stained with Mayer's Haemalum and Indigo carmine. The muscles are stained an intense blue, while the connective tissue through which they pass is light purple.

In still another specimen both the oblique muscles are present on the left and three of the rectus muscles, one of which, the interior, extends forward in the inner part of the orbit and joins the lower oblique as in the first individual described. No fibers of this muscle reach the eye. On the right side of the same individual the upper rectus and but one oblique muscle are present. In still other individuals not suitable for tracing the muscles their fluctuating number has been noted, and their varying method of attachment to the eye is also a matter frequently noticed.

Inside of the loose connective tissue surrounding the eyes there is a more compact sheath. This is thickest in front of the eye where it contains spherical nuclei and holds one to three compact cartilages which usually are disposed to form a hood over the front of the eye. These cartilages, described by WYMAN in this species and KOHL in rosae, and taken by the latter as the remnants of suborbital bones, have nothing whatever to do with the latter structures. Their nature can be understood from their close association with the eye, by the fact that they are closely bound together by the scleral connective tissue and by the fact that some at least of the eye muscles are attached to their outer surfaces. They are unquestionably scleral elements (*scl.c* in figures 30—41). There may be some hesitation in accepting this view of the nature of these cartilages since no cartilage whatever is found in the sclera of Chologaster. Their position, usually in front of the eye, is also anomalous if they are scleral cartilages. It may be stated, however, that the eye of Amblyopsis is not simply a miniature normal eye. The whole eye has collapsed with the disappearance of the vitreous humor and looked at in this light there is no difficulty in the position of the cartilages which have fallen together over the front of the eye. The presence of granular nuclei in front of the eye over the region of the iris has been noted by KOHL in Troglichthys and observed by me. These nuclei are probably the homologues of the nuclei found in the ligamentum pectinatum of Chologaster. See Cuts 1 und 4.

In shape, number and size the scleral cartilages differ very much. In one instance cartilages extend continuously from the exit of the optic nerve more than half way over the side and around the front of the eye. In another a single cartilage lies directly in front of the eye, and on the opposite side of the same individual a single cartilage lies behind the eye. The sclera is much more developed than in Chologaster. Consisting aside from the cartilages, of an abundant fibrous tissue.

The Choroid is a thin membrane closely applied to the eye. It contains a few oval nuclei parallel with the surface of the eye. It contains a few pigment cells irregularly scattered and not at all uniform in different eyes. The pigment cells are rounded masses usually much thicker than the whole of the choroid in regions devoid of pigment. About the entrance of the optic nerve is frequently a large accumulation of pigment corresponding with the increase in the amount of choroidal pigment in Chologaster at the same place. Even this mass is not uniformly present. Sometimes granular masses interspersed with pigment are found here which give one the impression of a degenerating mass, and especially large accumulation of pigment is found in the eye figured. Blood vessels are present in the choroid. They are apparently as great in relative capacity as in Chologaster. In an individual with the vascular system injected a vessel 0.01 mm in diameter approaches the eye with the optic nerve, but it does not enter the ball with the latter. It breaks up into smaller vessels distributed in the choroid. A vessel is usually found in a groove of the pigment layer of the retina. This groove extends along the dorsal wall of the eye; otherwise it might be taken for the choroid fissure. Figure 30 *cps.sng 1.*

A somewhat larger vessel than at other points is found near the iris where this structure appears to be continuous with a deep choroidal groove. Fig. 39 *cps.sng.* In the young a blood vessel enters the hyaloid cavity at this point.

The eye itself, exclusive of choroid and sclera, differs greatly both in size and inner structure although the general arrangement of the retinal cells remains the same in all cases. In some cases the pigment layer of the retina forms a large membranous bag many times too large for the enclosed structures which lie as a small ball in this comparatively vast cavity. In such eyes found in old individuals the wall is in many places free from pigment. In general the pigmentation of the retina varies inversely as the pigmentation of the choroid. In other individuals the eye forms a compact mass of cells (figure 32). To anticipate somewhat, the vitreous cavity with the hyaloid membrane and its blood vessels have entirely disappeared, the ganglionic cells have in large part been brought together into a solid mass, the lens has been very much reduced in size, the irideal opening has usually become closed.

Pigmented layer and Cones.

The pigment cells as they appear in the best preparations of the better developed eyes may be described first (figure 30). The cells are longest near the entrance of the optic nerve. They possess an outer segment, not determinable in all cells, which is free from pigment. They have a homogeneous, vesicular ellipsoidal nucleus situated near the outer end of the cell. This nucleus is strikingly different in shape and constitution from the same structure in Chologaster. It stains but faintly and then homogeneously. Just within the nucleus there is a well defined mass of dense pigment forming a cap over the inner side of the nucleus and at times encroaching on the rotundity of its inner outline. This pigment mass evidently has its counterpart in Chologaster where a solid band of pigment is found just within the nucleus. In depigmented cells this pigment cap is seen as a deeper staining, more dense protoplasm than the rest of the cell. From this pigment segment a prolongation, much poorer in pigment and containing a central uniformly staining core extends toward the interior of the eye. This core, which in reality extends also into the pigmented section, occupies the position of the cones in Chologaster. In no case have I been able to trace any connection between these bodies and the outer nuclear layer. They are sometimes in several segments or in a number of spherical bodies and occasionally two are seen side by side in the same cell in tangential section. In position they certainly suggest cones and this suggestion is heightened by the presence in the inner end of some of the cells of a vesicular structure very similar to the nucleus, but frequently with an angular indentation on the surface. These occupy the relative position of the cone bodies, they are by no means found in all eyes. The evidence seems to point most strongly in favor of the supposition that they are cones. One of the cells measures as follows: diameter of cell 0.007 mm, nucleus 0.007 by 0.007 mm, deeply pigmented mass 0.007 mm, total length of cell 0.036 mm.

No rods have been found.

Iris.

The pigment cells decrease in height towards the irideal portion of the eye where they are replaced by a layer of pigmentless cells forming a thin membrane (in figure 30). The nuclei of these cells stain darker than the bodies of the cells which is the reverse of the conditions seen in the pigmented cells. In individuals up to 35 mm long similar cells extend along the line of the vanishing choroid fissure, figures 33 and 38.

The pigmentless membrane is apparently the relic of the outer pigmented layer of the iris. If so it has undergone greater changes that the rest of the pigmented layer, for it is well pigmented in all the species of Chologaster.

The inner layer of the iris is frequently entirely separated from the outer layer and not infrequently is entirely obliterated. (A few rounded pigment masses are always found within the eye at this point.) In other individuals a minute opening is still present and the outer layer of the iris is continuous with the inner which contains some of the elongate nucleated cells found in the region of the ora serrata in Chologaster. These are much more regularly present in Typhlichthys subterraneus. These nuclei are variously grouped in different eyes as is represented by the figures 30, 31, 34, 36, 38 and 40. The exact significance of the various structures about this region in the eye can not always be determined owning to their presence or absence in different individuals and their great variability when they are present. In this region are sometimes a few cells with elongate nuclei that cannot be identified with any of the structures considered. These may represent all that is left of the hyaloid. Blood vessels do not enter the eye in the adult.

Between this pigmentless membrane and the rest of the retinal structures, i. e. within the pigment epithelium there is in the majority of the adult eyes an irregular mass of pigmented cells. I am entirely at a loss to account for this mass unless with the shrinking of the eye as the result of the loss of the vitreous body and lens and the consequent closing of the pupil, the margin of the iris was rolled inward and some of the pigmented cells of the outer layer of the iris came to lie within the eye after the closing of the pupil. The iris is seen to be rolled in the way imagined in many sections of Chologaster and the method of the closing of the pupil in Typhlomolge is as I have suggested (*f* page 587).

In many individuals, and strikingly so in two specimens 25 (Fig. 32 *am*) and 35 mm long (Fig. 34) respectively, deeply staining spherical bodies, much smaller than the nucleus and staining much deeper, are present in the pigment cells. Those stained with haemalum are quite dark and give the appearance of a large centrosome.

These I take to be myeloid bodies noted in the pigment cells of the frog and other forms.

In most individuals the high development of the pigmented region, above described, is not found. In some individuals the pigmented layer is composed of flat pavement cells forming a large vesicle. In others the pigment is either entirely absent or very sparingly developed. As mentioned above the pigmentation of the eye seems to vary inversily with the pigmentation of the surrounding structures.

The pigment is in all cases granular and differs in this respect from the prismatic pigment of the eye of Chologaster.

The nuclear layers.

Within the pigment and cone layer lies a nuclear layer made up of about four series of cells (*3*—*7* in figures 30—37). The nuclei reach from 2½—3½ in diameter. Rarely I have succeeded in staining the smaller nuclei different from the larger. They are, in such cases, more refringent, the large nuclei being granular. The larger nuclei may be the spongioblasts. In a young individual this difference was well marked. Here the smaller cells were confined to the proximal part of the eye, figure 32.

A separation of the nuclear layer into an inner and outer with an intervening outer reticular layer I have noticed but once. In this eye a slight separating space was found on one side, and here there were one or two cells that may be fulcrum cells. If so it is the only indication of this layer in all the preparations made. The suppression, partial or total of the separation into an outer and inner layer, has also been noted by Ritter in Typhlogobius.

The inner reticular layer.

The inner reticular layer is always well developed; occasionally a few nuclei extend partially in from the outer nuclear layer. It is frequently thicker on the dorsal half of the eye (figure 38) than on the ventral half, but sometimes the reverse. In figure 30 the ventral half is but 0.012 mm. Nuclei have but once been found in this layer, and I have not been able to identify Müllerian nuclei as such either in this or the nuclear layers.

The ganglionic layer forms a compact mass of nuclei, somewhat funnel-shaped, with the narrow end toward the exit of the nerve (*9* in figures 30—38). I have found from 60—125 nuclei in this mass.

At the wide end of the funnel this mass of cells is directly continuous with the cells of the nuclear layers. The cells in this intermediate layer are of the large type, and as they give off fibers to the optic nerve they may be classed as ganglionic or possibly as cells belonging to the spongioblasts.

Optic nerve and Lens.

The optic nerve is always evident in the eye itself except in very old individuals. It passes as a compact thread through the pigmented layer into the ganglionic layer. Here it breaks up into smaller bundles, the fibers of which pass in part to the cells within the ganglionic core, while the greater part pass to the large cells at the outer rim where the ganglionic cells pass over into the cells of the granular layers. The fact that these large cells give off the greater part of the optic fibers suggests whether or not these cells are really the ganglionic cells, while the cells forming the core are such cells as are seen at the entrance of the optic nerve in Chologaster (Fig. 3) and there form a plug arround which the optic fibers pass directly to the ganglionic cells. The bundles of fibers passing to the anterior cells never pass through the mass of core cells but at one side of this mass. In the right eye of an individual 25 mm long they pass out in front of the mass; in the left eye of the same individual behind them.

Outside the eye itself the matter of following the optic nerve becomes a much varying task. In very young, and up to 25 mm, there is no difficulty in tracing the optic nerve to the brain. In newly freed individuals[1]) the optic nerve passes nearly obliquely down and in, while in an individual 25 mm long it passes horizontally back and in toward the foramen for the optic nerve. In the latter individual the nerve leaves the eye not as might be expected at the posterior inner face, but at the anterior inner, making a sharp turn as it leaves the eye. Its compact nature is entirely lost after leaving the eye, forming a loose bundle several times as thick as the optic nerve within the eye. It is here surrounded by a very thin film of pigment which in its turn is surrounded by layers of fibrous tissue.

In individuals much more than 25 mm long it is no longer possible to follow the nerve to the brain. It can be followed some distance, but usually disappears before reaching the optic foramen. In but one instance did I succeed in following it into the brain cavity in an adult specimen. The structures surrounding the optic nerve are as variable as those surrounding the eye. In one case it is surrounded by various layers of pigment, while in others scarcely any pigment is found with it.

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[1]) About two months old.

The most highly differentiated lens was found in an individual 130 mm long, i. e. a very old one. The lens in this case consists of a few nuclei about which there are concentric layers of a homogeneous tissue (figure 8). In other individuals structures approaching this condition were found (figure 9). In one a large cell, in another a cell with concentrically arranged lamellae. The lens, in an individual 25 mm long, could not be found at all, and in another 35 mm long could not be determined with certainty. The relative development of the lens is not dependent on age. The lens described by WYMAN was undoubtedly one of the scleral cartilages, for these cartilages are frequently nodular in this species, and one usually lies in front of the eye.

The supposition of WYMAN that one of the scleral cartilages is the lens need not be criticized too severely. The structures described above as the lens are considered such more, because they could not be identified as anything else, and because nothing else that could with certainty be considered a lens could be found aside from these structures rather than on any direct evidence. The development of the eye would indeed lead one to suppose that the lens is actually placed entirely outside the optic cup, and in that case none of the structures here described can be the lens. With as much variation as is found in all the structures it is not improbable that the lens may in some individuals be found within the optic cup, and in others outside of it.

The many varied details in the eye is in striking contrast to the condition in normal fishes. The great variety in structure suggests the paradoxical idea that every eye has been individually operated upon and healed in an individually peculiar manner.

The eye undergoes progressive ontogenic degeneration after maturity. In an individual 130 mm long the pigment about the eye becomes more prominent and the connective tissue much increased. The pigmented layer forms on one side of the largest individual a large vesicle in which the remainder of the tissues are but an irregular, ill-defined mass, and in the eye of the other side even this degree of definitness is lost. The only thing suggesting an eye is the presence of pigment, optic muscles and scleral cartilages.

Measurements of the eye of Amblyopsis in μ.

Length of fish	Diameter of eye axial	Diameter of eye vertical	Pigment layer posterior	Pigment layer anterior	Nuclear layer	Granular layer	Ganglionic layer
25 mm	160 μ	160	28	?	16	24	12
60 mm	144	108	36	20	16	24	
60 mm	96	108	28	12	12	28	
75 mm	56	142	56	4	12	21	12
85 mm	204	108	16	4	12	22	
108 mm	200	142	56	8	10	54	
108 mm	?	84	52	4	13 × 120		
Averages			39	$8\frac{2}{3}$	13	21	12

6. The Eyes of Typhlichthys subterraneus. Girard. (Figs. 12—49.)

The eye of this species has not heretofore been made the subject of study.

The following account is based on three specimens 20, 25, and 45 mm long respectively, from a small cave in the town of Glasgow, Ky. and a number of specimens of various sizes, the largest 54 mm from Mammoth cave, Ky. These were all collected by myself in the early part of September, 1897.

The eye of this species is in general less degenerate than that of Amblyopsis. The accessory structures are, on the other hand, much more degenerate than in Amblyopsis.

The eye can not be seen from the surface. The region of the eye is, however, more conspicuously apparent than in Amblyopsis on account of the thinner tissues of this smaller species through which the orbital fat-mass can be seen. The eye can not be seen even in heads cleared with oil on account of the almost total absence of pigment about the eye and its total absence in the eye itself.

The eye is surrounded by a large mass of fat through which connective tissue cells are scattered. A distinct separation of the orbital fat from the other fatty tissues in this neighborhood by connective tissue membranes such as are found in Amblyopsis is not noticeable in this species. A few pigment cells are found scattered through the fat-mass. They are nowhere massed together so as to become evident to the naked eye. In one eye not a single pigment cell is found about its surface, in another three are found on the surface of the connective tissue surrounding the eye. In no case is the pigment about the eye of any significance, for it is as abundantly found throughout the fatty tissue surrounding it.

No trace of eye muscles are present in this species. Scleral cartilages are entirely absent, a condition in striking contrast to that found in Troglichthys rosae with which this species has been confounded.

Sclera and choroid.

The sclera and choroid coats are not separable in this species. In specimens up to 10 mm in length the eye is surrounded by a very thin membrane containing here and there a nucleus, and in the region of the choroid fissure and near the exit of the optic nerve a few capillaries. In the oldest specimen, 54 mm long, the tissues about the eye are distinctly more fibrous, but even here I have not been able to separate the layers. From the front of the eye a strand of tissue similar to that surrounding the eye extends outward. A blood vessel reaches the eye with the optic nerve, and a few capillaries are found on the surface of the eye and in the hyaloid membrane, but the details of their distribution I have not made out. This primitive condition of the outer layers of the eye are not so striking as they first appear when the conditions in Chologaster are taken into consideration, for even in Chologaster the choroid and sclera are insignificant.

The eye ball.

The eye is on an average 1.68 mm in diameter and has reached this size when the individual has reached 25 mm in length. In specimens of this length the cells of the retina are still undergoing division. In a specimen 20 mm long it has a diameter of 1.12 mm. Its maximum differentiation is not reached at the time it first reaches its maximum diameter. The eye is probably potentially functional throughout life as a light-perceiving organ. A minute vitreal cavity, remnants of the hyaloid with its blood vessels, outer and inner nuclear as well as inner and usually also the outer reticular layers are well differentiated and the optic nerve is certainly still connected with the brain at a time when the fish has reached a length of 40 mm.

The position of the eye is not fixed so that in different series of sections presumably cutting the head in the same planes, the choroid fissure occupies various positions and the eyes are cut in various directions. With this general sketch the various layers may be taken up in detail.

Pigment layer. *1* in Figs. 42—49.

No pigment granules are present in the eye, a condition in great contrast to that in either Amblyopsis or Chologaster where the pigment is least affected by the degeneration processes. The absence of pigment in this eye is indeed unique among vertebrates, Ucke '91, pag. 15. Whether pigment is developed in earlier stages and disappears I have not been able to determine.

In the specimens 40 mm and less in length the pigment layer consists of a series of cells, but little separated from the underlying outer nucleated layer. The separation between the layers is greatest near the exit of the nerve and at the iris. In older individuals a considerable space is formed between the pigment layer and the outer nucleated layer on the dorsal and proximal parts of the eye, but since in all the cases under consideration a good share of this space is attributable to reagents, a more detailed description is useless. However in these regions delicate protoplasmic processes extend inward to the nucleated layer. The nuclei of the pigmented layer stain much more faintly than those of the rest of the retina with Biondi-Ehrlich, but just as deeply as the others with Haemalum. The cells of the pigment layer are in one series, but occasionally a cell is found below the niveau of the rest.

A few cells very elongate in section may be mentioned here. They were found (Fig. 41) on the inner face of the pigment layer and marked *x*. These are important in the interpretation of the structure of the eye of Troglichthys rosae where they are also found. Their origin and significance are not known.

Rods and Cones with their nuclei.

While the outer nuclear layer is very well developed indeed, the rods and cones are not definite. In the most highly developed eye there is a distinct outer limiting membrane. Without this are filmy processes continuous with those from the pigment cells. Very rarely one sees an elliptical, slightly granular body which may or may not be a cone body. The outer nuclear layer is in some cases quite distinct, consisting of a compact series of outer (cone!) nuclei, irregularly elliptical in outline, below these are a few cells of a second series (rod nuclei?) sometimes with their longer axes parallel with those of the outer layer, sometimes horizontally disposed.

Cells of bizarre appearance were noted near the iris in one of the younger individuals (45). Some of these are long club-shaped, rounded end turned inward, others the reverse, still others with long elliptical outer segments and smaller inner segments.

The cones are certainly less developed than in Amblyopsis, while the reverse is the case with the nuclei belonging to them.

The outer nuclear layer seems but little more degenerate than in Chologaster as far as differentiation is concerned, being of course very much more limited in extent.

Outer reticular layer. (*4* in the figures.)

A distinct break between the outer and inner nuclear layers, of varying thickness, where nuclei are absent or few and far between, is present. A distinct boundary line for this layer does not exist and a reticulate appearance is only to be seen in short stretches, otherwise the layer is only distinguished in the preparations by the absence of nuclei. In the younger specimens examined this layer is not differentiated, the nuclear layers forming one continuous structure. It is quite evident from this that tissue differentiation is not completed in the eyes of this species till very late.

The inner nuclear layer.

The nuclei of the inner layer are of two sorts, larger, granular, more faintly staining ones, and smaller, more homogeneous, deeper staining ones. In one individual (Fig. 49) they are seen to be surrounded by a comparatively large cell-body whose outlines are made distinct by the branches of the Müllerian fibers. In thickness this layer exceeds both the nuclear layers in Amblyopsis. Nuclei belonging to the Müllerian fibers I have not been able to identify as such. Supporting fibers can be followed in some individuals from the ganglionic layer through the inner reticular and the inner nuclear layers, in which they branch to send processes between the regular cells (Figs. 48 and 49). Once peculiar horizontal nuclei were noticed on the inner face of this layer. They are marked *y* in Fig. 44.

The inner reticular layer.

Horizontal cells are not present in the inner reticular layer. Otherwise the layer offers no peculiarities. Owing to the persistance of the union of the lips of the choroid fissure and the consequent merging of the ganglionic into the outer layers at this point, the inner reticular layer appears horseshoe-shaped in a vertical longitudinal section (Fig. 44). In a section going through the plane of the choroid fissure (Fig. 42, 8) it appears as a central area in the eye, free from nuclei. This condition, which is seen in all but the eyes of the oldest individuals, is of importance in interpreting the conditions seen in Troglichthys rosae. In the older individuals the nuclear layers become thin on either side of the choroid lips, and the reticular layer approaches the pigment layer (Fig. 49). The layer is well developed, its relative thickness may be gathered from the comparative table.

The ganglionic layer.

There is no distinct optic fiber layer. The ganglionic layer consists of a single layer of cells irregularly disposed about the vitreal cavity where this is present and forming a solid core of cells behind the vitreal region enclosing blood-vessels and hyaloid nuclei. Some of the cells appear to send fibers into the inner nuclear layer in the older retinas, these may be Müllerian nuclei since in Chologaster cornutus such are found in this layer. The total number of nuclei counted in one example as belonging to this layer is 100, not very greatly different from the number noticed in specimens of Amblyopsis. In specimens up to 40 mm in length the choroid fissure is a well marked structure. The pigment layer and inner layers merge into each other here, and the ganglionic layer is continuous with the pigment layer. As stated above, the inner reticular layer does not surround the ganglionic layer at this point. A vertical longitudinal section of the eye has the general appearance of a section through a Graafian follicle (Fig. 44). The ovum would correspond in position to a cell in the ganglionic layer, the stalk of the ovum to the lips of the fused choroidal fissure, the outer follicular cells to the nuclear layers and the interior cavity of the follicle to the inner reticular layer of the eye.

Optic nerve.

The optic nerve is not as distinct at its exit from the ganglionic layer as in Amblyopsis, but in specimens even 40 mm long there is no difficulty in tracing it to the brain. In specimens of the latter size it has a diameter of 9 μ. It contains many elongated nuclei, some of which are also seen with the optic fibers within the eye (Fig. 46).

The covering of the optic nerve partakes of the same indefinite nature as that of the eye itself with which it is continuous. No pigment accompanies the nerve as a distinct layer, but here and there as in the covering of the eye a pigment cell may be seen, while about its entrance into the brain cavity some pigment cells are also found.

Epithelial part of the iris.

The pigment cells, as in Amblyopsis, decrease in height towards the irideal portion of the retina, where they become a series of pavement cells with rounded nuclei directly continuous with a layer of cells with elongate elliptically nucleated cells forming the inner layer of the iris. The homologues of the elliptically nucleated cells are found in the iris of Chologaster in the region of the ora serrata. At the junction of the outer and inner layers of the iris the cells are sometimes heaped up making the irideal margin quite thick (Fig. 48 and 43). There is in some cases a distinct free pupil, while frequently the opening is directly continuous with the choroid fissure which may remain open in this region (Fig. 49).

Lens.

The lens was not found in all eyes, when present it is situated at the anterior end of the choroid fissure or behind the iris. It consists of but very few cells. These cells are undifferentiated. No fibres or other signs of differentiation are at all evident. The lens cells are not distinguishable from the neighboring cells, and only the faint lines seen to surround the group serve to distinguish them.

Vitreous body and hyaloid.

The choroid fissure is distinctly evident in specimens at least 42 mm long, not as a distinct fissure, except in front, but as a line along which the various nucleated layers of the retina are merged. In the distal part of the retina the fissure is not entirely closed and it here leaves an opening into the vitreous cavity which is more distinct and larger in the large specimens than in the smaller ones (Fig. 49). The vitreous cavity when present at all is confined to a very narrow region just behind the lens. Here a few oval nuclei and an abundant supply of blood vessels are to be found (Fig. 49, 43 and 48), the latter communicating with the exterior through the open part of the choroid fissure. The vitreal body or cavity does not extend far into the eye, and in the core of ganglionic nuclei, where the vitreal cavity does not extend, the hyaloid membrane is represented by blood corpuscles and by a few cells with elongated nuclei whose longer diameters are parallel with the optic nerve.

Measurements of the eyes of Typhlichthys subterraneus.

Length of fish	Diameter of eye axial	Diameter of eye vertical	Pigment layer	Nuclear layer	Reticular layer	Ganglionic layer
20 mm	142 μ	120	24	28	22	7
25 mm	160	142	—	—	32	—
25 mm	180	160	40	36	20	—
40 mm	180	144	12	36	18	12
42 mm	160	120	20	28	16	8
42 mm	160	142	16	32	12	28
Averages	162.66	128	22.4	32	20	13.75

7. The eyes of Troglichthys rosae, Eigenmann.

In December, 1889, Garman '89 published an account of cave animals collected by Miss Ruth Hoppin in Jasper county, Missouri. Among them were a number of what were supposed to be Typhlichthys subterraneus, Girard. A comparison of the eyes of two of the specimens collected by Miss Hoppin with the eyes of specimens of Typhlichthys subterraneus from Mammoth cave showed that the western specimens represented a distinct species, and that Kohl '92 must have based his account on specimens from Missouri. The latter fact was later confirmed by Dr. Mark who had furnished Kohl his specimens.

In the Spring of 1897 I visited the caves examined by Miss Hoppin, at Sarcoxie, Mo., but as my stay was limited and the caves were full of water I did not succeed in getting any additional material. In September, 1898, through a grant from the Elizabeth Thompson Science Fund I was enabled to make another and this time successful effort to secure this highly interesting material.

Kohl '92, page 59, described the eyes of Typhlichthys basing his account on two specimens respectively 36 and 38 mm long. Dr. Mark informed me that at least one of these specimens came from

Missouri, and KOHL's account was certainly drawn from Missouri specimens only.

He found that the bulbus is nearly spherical, with a diameter of 0.04 mm. The orbit is a very flat cavity that offers little protection to the eye. Suborbitals are totally wanting and in their place is a cartilaginous protecting capsule, placed over the bulbus dorsally and laterally, and made up of several cartilaginous plates 0.02 mm thick. Between the plates the connective tissue frequently contains thick and large nuclei which are sometimes united into groups. One such mass he thinks has been taken for the lens by WYMAN '54 (PUTNAM Fig. 5). It lies 0.195 mm from the outer surface of the epidermis. All tissues covering the eye show absolutely no difference from neighboring parts. Eye muscles are not found, but sometimes there are stiff connective tissue strands connecting the cartilaginous bands with the tissues immediately surrounding the eye. The eye in the specimens examined he considers in the stage of the formation of the secondary eye vesicle. There is still a large cavity present representing the primitive eye cavity which is only being encroached upon by the invaginating outer cells, which in part are precociously ganglionic, sending each a process to the optic stalk. The optic stalk no longer shows a cavity, which he assumes became obliterated by the direct ingrowth of nerve fibrils and not in the usual way. The invagination of the inner layer may have progressed further in one eye than in the other, but there is always a considerable space still left between the inner and the outer layers of the primitive eye vesicle. The elements of the inner layer, the ganglionic cells, he found to send their processes directly inward. They must have gradually revolved, since in the normal eye the nerve processes are directed outward. Some of the fibers cross each other on their way to the outlet for the nerve. Not all of the invaginated cells send processes. Among those that do there are smaller, round cells without a trace of fibers. From these the rest of the nervous parts of the retina, including of course other ganglionic cells, would probably have arisen. The outer layer of the secondary eye vesicle is also single layered. The cells are elongate, with oval nuclei, and without a definite arrangement. They are connected with the few cells of the optic stalk that still remain. Connective tissue cells are found in the n. opticus. They are probably mechanically active in degeneration by separating the elements. He found no sheath to the optic nerve as described by WYMAN. The lens he found to be a spherical cell heap 0.01 mm in diameter in the distal pole of the eye. It lies just within the sclera and the cup of invagination. The sclera is made up of several layers of very fine fibrillae. Nuclei are not found in it, but nuclei are found on its outer surface. No vessels are found in the choroid which consists of connective tissue cells more numerous on the dorsal than on the ventral surface. The Typhlichthys eye is »absolut pigmentlos«. The surrounding tissues are rich in pigment which, however, is not related to the eye. There are pigment masses here and there, but especially between the bulb and the cartilaginous capsule.

It is hard to arrive at a proper explanation of the structure of this highly degenerate eye even with an abundance of material, and it is probably not to be wondered at that Kohl in the work outlined above did not see the eye muscles, mistook the sclera for suborbitals, parts of the retina for the choroid, interpreted the pigmented epithelium of the eye as an extra optic pigment mass, mistook the inner reticular layer for the primary optic cavity, the nuclear layers for the pigment epithelium etc. etc., and arrived at a thoroughly erroneous idea of the general structure of the eye, and permitted this erroneous conception to lead him to absurd theories on the degeneration of eyes in general. The invaginating cells of the primary optic vesicle are supposed to have been directly converted into the ganglionic cells which are usually among the very last products of the histogenesis of the retina[1]).

By supposing that the eye was arrested at the beginning of the invagination, and that the invaginating cells rotated on their axes and were converted directly into ganglionic cells, Kohl derived the nucleated layers from the outer pigment producing layer of the primary vesicle at the same time ruling the pigment layer out of the eye.

The eye is very small and situated so deep that it is impossible to see it from the surface (Fig. 9*a*). In the upper half of a head cleared in xylol it is just evident to the naked eye as a minute black dot (Fig. 9*e* and *f*). As in Typhlichthys and in Amblyopsis it is surrounded by a fat mass filling the orbit. It is not at all uniform in shape in different individuals or even the two sides of the same individual. It can be located and seen in cleared heads solely on account of the pigment which is always abundant over the distal face of the eye. It is located so far beneath the surface as to occasionally lie in contact with the brain case nearly opposite the posterior end of the olfactory lobe. It has thus been withdrawn much further than in the other blind species.

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[1]) The mistakes of Kohl, especially as far as they are the result of criticising work done on Amblyopsis while he was working on another species seem to me to point a moral. A certain species must not be too readily taken as an exponent of a family, order or class, and a knowledge of related species and geographical distribution is not altogether to be neglected.

It is very much smaller than the eye of either T. subterraneus or Amblyopsis. Its size is, however, quite variable, measuring 40, 49, 56, 64, 54 by 96, 56 by 120 in different instances, exclusive of choroid and sclera.

The muscles of the eye were in no case normal. I have not found more than two rectus or more than one oblique muscle belonging to any one eye. They can best be made out from horizontal sections. In cross sections it is very difficult to identify or follow them.

The best developed rectus was found in a specimen 35 mm long. It is composed of a number of normal fibers forming a bundle 20 μ in thickness, and from its origin to its insertion it is 256 μ long. The remarkable peculiarity of this muscle is that 100 μ of this is a tendon 4 μ in thickness (Fig. 50 *msc*). The tendon spreads into a cone-shaped mass of fibers attached to the proximal face of the eye. Traces of two muscles were made out connected with the right eye of another individual.

The oblique muscle is attached by a tendon to the face of the eye opposite that of the attachment of the rectus (Fig. 51 *msc*). In the best developed condition it was found to be but 9 μ in diameter, taking its origin at a point on the level of the lower surface of the olfactory nerve where the latter pierces the ethmoid and 160 μ laterad from it. The muscle itself is in this instance about 200 μ in length and is attached to the eye by a tendon of equal length. The rectus in the same individual is 208 μ long.

In all the cases enumerated above the muscles of the opposite side were not nearly so well developed. In the one with the well developed rectus the oblique was indistinct, while in the one with the well developed oblique the rectus is also well developed, but the striations are not distinct.

The scleral cartilages form one of the striking features of this eye. They are quite variable, forming a more or less complete covering for the eye. In cases they are several times as long as the eye and in such cases extend much beyond the eye. In one eye 49 μ in diameter the length of one of the cartilages reaches 160 μ (Fig. 53). They have not kept pace in their reduction with the reduction of the eye in size. As a consequence individual cartilages either extend beyond the eye or are bent at acute angles in their endeavor to apply themselves to the shrunken eye (Fig. 51 *scl.c*). These cartilages were mistaken for the suborbital bones by Kohl. There is absolutely no ground for this supposition. The suborbitals are present (Fig. 9 *a*) and widely separated from these cartilages. Further, the eye muscles are attached to the cartilages and to similar ones in Amblyopsis.

The presence of these large cartilages is the more remarkable when we consider that none are found in Typhlichthys subterraneus, and in the species of Chologaster, which in other respects resemble Typhlichthys in all but the development of the eye and the color. It is quite evident that Troglichthys and Typhlichthys are not derived from a common ancestor (except, of course, remotely). Their present superficial resemblances are the result of converging development under similar environments. A species similar to Chologaster agassizii gave rise to Typhlichthys subterraneus. What the ancestry is of Amblyopsis and of Troglichthys is not known. The cartilages are bound together by an abundant fibrous connective tissue containing a few corpuscles. (These I have found nowhere as abundantly as represented by Kohl.)

The choroid, in so far as this layer can be distinguished from the sclera, consists of a dense layer of fibers closely applied to the eye. Over the distal surface it is split into two layers between which there are a greater or smaller number of pigment masses (Fig. 52 *ch*). These would prove an effective structure to prevent the performance of the natural function of the eye were it functional. Pigment cells are much more sparingly found in other parts of the choroid. Blood vessels are very few in number, a condition to be expected in such a minute organ. This layer was mistaken for the sclera by Kohl.

The eye proper of Amblyopsis was found to differ very greatly in different individuals, but in general it maintains a certain degree of development from which the many individual variations radiate. The eye of Troglichthys rosae has similarly a general type of structure that is maintained but with many variations. This type is more degenerate than that of either Amblyopsis or Typhlichthys subterraneus. The eye of Troglichthys has been derived from an eye like that of Amblyopsis by the disappearance of pigment from the posterior part of the retina and the reduction of the central mass of ganglionic cells to the vanishing point. In the most highly developed eye of T. rosae I found but three of these cells. Both in size and in structure the eye of T. rosae is the most rudimentary of vertebrate eyes so far known, except that of Ipnops which is said to have vanished.

The vitreous cavity and the hyaloid membrane have vanished. The eye has collapsed, the margins of the iris have probably fused, and the pigmented and inner layers of the iris separated from each other. With this general sketch the elements of the eye may be taken up in detail.

1. Pigment layer: This layer is variously developed (*cf* in the figures) and may be quite different on the two sides of the head. One peculiarity is practically always present and very striking. The layer forms a covering over the distal face of the eye where, a priori, there ought to be no pigment, and is thinnest or absent over the proximal face where it ought to be most highly developed. Kohl has cut the Gordian Knot by excluding this pigment from the eye entirely by the choroid [sclera], but there is certainly no such membrane intervening between this pigment and the rest of the eye as Kohl has figured. On the contrary the choroid very clearly surrounds it, and from its own epithelial structure there is no room for doubt as to its nature. As said, its extension over the sides and back part of the eye differs materially in different eyes. In a number of instances no pigment cells are present either on the sides or at the proximal surface; in others the sides are well covered. If by any means the tissues of the eye are separated from each other the space is always formed between the pigmented layer and the rest of the eye. Processes are at such times seen to extend down from the pigment cells toward the rest of the retina. The cell boundaries and nuclei of the pigment cells are for the most part distinct. The cells are deepest over the distal pole of the eye and from this point they decrease in size to the proximal pole. Toward the upper face where the pigment epithelium approaches the lens the densely pigmented cells are transformed into much thinner pigmentless cells. These are probably the homologues of the pigmentless cells over the distal face of the eye of Amblyopsis, and, if so, are all that is left of the outer layer of the iris.

The explanation of the condition of the pigment epithelium in this eye presents more difficulties than any other structure. In the eye of T. subterraneus no pigment is developed, but the pigment epithelium is normally developed. In this eye pigment is formed in the cells that are present, but the epithelium has anything but a normal structure. The pigment cells in the proximal face of the eye have either disappeared or been displaced. The only other alternative, that they are present but without pigment and indistinguishable from the cells of the outer nuclear layer while possible is scarcely probable, for in many eyes there is but a single layer of cells representing all of these structures, and in other cases even these have vanished. The objection to the idea that the cells have vanished is to be found in the fact that they are so well developed over the distal face. This point can only be settled by a study of the development of the eye, but one other suggestion may not be out of place. A comparison of this eye with that of Amblyopsis will suggest the homology of the anterior cell mass in the latter case, with the pigment cells always present between the retina, and the irideal pigment layer in the former species. This correspondence is further strengthened by the fact that frequently the pigment in T. rosae over the front of the eye is in more than one layer of cells. Since, however, I was unable to arrive at an entirely satisfactory explanation of the origin of this pigment mass in Amblyopsis, it will not help us much, should the two structures be homologous.

Attention may be called here to the fact that both in Amblyopsis and in the present species the lens — and therefore the lost pupil — are not situated at the distal pole of the eye but above this point, and that both in regard to the pupil and the eye in general the location of the two pigment masses is the same.

The pigment is granular, not prismatic.

The lens: This is the only structure of the eye concerning which Kohl has not made any mistake. It is a small group of cells closely crowded together and about 10 or 12 μ in diameter (Figs. 54*a* and 55). There are no indications of fibrilation or the result of any other histogenic process; it appears as an aggregation of indifferent cells. On its surface there are at times cells that are evidently of an epithelial nature being flattened so that their sections appear much longer than deep. It lies at the upper outer face of the eye at the margin of the pigment mass decribed in the last section. It is not covered by pigment or other retinal substance. Kohl considered this condition a primary one. The lens, however, does not lie in an incipient secondary optic cavity, the vitreal cavity, as KOHL supposed, but in the remains of such a structure. Under the circumstances it is doubtful whether the uncovered condition is primary. It seems more probable, considering the condition in Amblyopsis, that the lens was enclosed by the closing of the pupil over the eye, and that the present naked condition is the result of the subsequent degeneration of the iris over it. That the latter is the phylogenic origin of its present condition there is no doubt.

The retina: The elements of the retina proper, i. e. the ganglionic, nuclear and reticular layers form a vesicle arranged so that the cellular elements surround a central (the inner) reticular layer. These may be taken up seriatim. The cellular elements are of three sorts.

1. Behind the lens and behind the pigment layer, sometimes also over the side of the retina, lie a few cells with elongated nuclei (Figs. 52, 53, 54 and 56) and so arranged as to suggest an epithelial covering for the underlying structures. Some of these cells were by KOHL supposed to represent the choroid with which they have absolutely no connection. It is possible that some of these lateral cells are modified pigment cells, but even this seems doubtful. I am unable to refer the cells of this nature situated laterally over the retina to any structure in the normal retina. Such cells are, however, found in the eyes of T. subterraneus between the pigment epithelium and the nuclear layers (in Fig. 44), and whatever their origin the two structures are unquestionably homologous in the two eyes. It is probable that the cells with elongated nuclei to be found behind the lens are of different origin and significance. They may be the remains of the elongated cells found in the inner surface of the iris of Chologaster, cells which are still present in both Amblyopsis and T. subterraneus. It is also possible that they are the remains of the hyaloid nuclei.

2. The ganglionic cells, which in Typhlichthys are arranged around the vestige of the vitreal cavity, and in Amblyopsis form a central core, and are distributed over the front of the retina, are in this species practically confined to the latter location. All there is left of the central core of ganglionic cells in Troglichthys rosae is three cells in the most highly developed eye found (Fig. 56). In the other eyes no indication of these cells was found. If these cells come to be formed at all in the present eye they migrate forward

where they form the anterior wall of cells surrounding the inner reticular layer. The fibers of the ganglionic cells extend directly from the ganglionic cells through the reticular layer to the exit of the optic nerve. The cells must, as KOHL has suggested, have undergone a rotation on their axes to send their fibers directly to the optic nerve, unless only the lineal descendents of those ganglionic cells immediately surrounding the entrance of the optic nerve in Chologaster are here represented, a supposition not to be entertained. The ganglionic nuclei are occasionally notably larger than the nuclei of the rest of the retina, but they are by no means always so.

3. The cells of the nuclear layers join those of the ganglionic layer. The cells of the inner and outer nuclear layer and the horizontal cells are indistinguishable from each other. They form, in the most highly developed condition, Fig. 9, *3—7*, a layer three cells deep covering the sides and the proximal surface of the inner reticular layer. In some cases the layer is reduced to a single series of cells, and even these are occasionally absent (*3—7* in Figs. 50—56). There is no sharp distinction between the nuclei of this layer and those of the ganglionic layer, so that the boundary between these cells and the ganglionic cells is not marked. In some instances these cells appear to be directly continuous with the cells surrounding the origin in the optic nerve. This condition lead KOHL to imagine that the primary optic stalk had become filled with nerve fibrils.

The reticular layers: The outer reticular layer is not developed. The inner reticular layer forms, with the optic fibers traversing it, the spherical or pear-shaped central mass of the retina. No cells are developed in the reticular layer. The optic fibers appear to pass directly through the reticular layer. This condition is probably apparent rather than real. First the vitreous cavity disappeared bringing the ganglionic cells and the optic fiber layers together in the center of the eye. This condition has just been reached by T. subterraneus and Amblyopsis. In the present species the ganglionic cells have disappeared from the center, and only the optic fiber layer remains. This is represented by the individual fibers passing from the ganglionic cells to the exit of the optic nerve. They do not form a compact nerve, but the fibers pass individually to the exit in the most direct route from their respective cells.

I have been unable to trace the optic nerve for any distance beyond the eye. In one case it leaves the eye as a loose bundle 12 μ in diameter; in another case it is more compact, being but

4 μ in diameter. It is surrounded by a sheath of varying thickness and complexity. In one case there are a few cells about the nerve, and these are covered by the tendon of the rectus muscle which forms a complete covering.

Measurements in μ: The scleral cartilages vary from 18 to 40 in thickness.

The distance from the distal face of the retinal pigment to the ganglionic cells varies from 30 to 40.

The pigment cells have a maximum depth of 14, dwindling from this to 2 or 3 on the sides.

The nuclear layers reach a maximum thickness of but 10.

The inner reticular layer, including the optic fiber layers, is about 40 in all directions, reaching a proximodistal length of 70.

The lens measures from 10 to 15.

II. General Part.

As in all organs no longer of use or hindrance, and therefore no longer under the control of Selection, the individual variations in the structure of the eye of Amblyopsis, Troglichthys and Typhlichthys are very great. There is also a marked change in the eye with age. It is therefore necessary to distinguish between individual variations and stages in ontogenic and phylogenic degeneration. The eye of each species has a general structure which is typical for the species. The individual variations have been sufficiently described under the respective species.

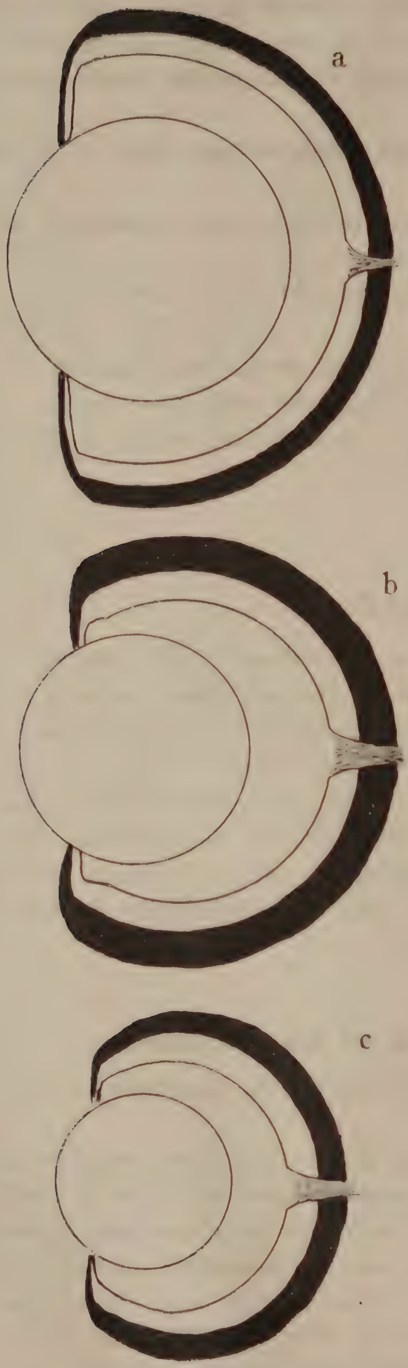
1. Phyletic degeneration of the Eye as a whole.

The steps in degeneration are indicated in the accompanying text-figures and in figures 57—61.

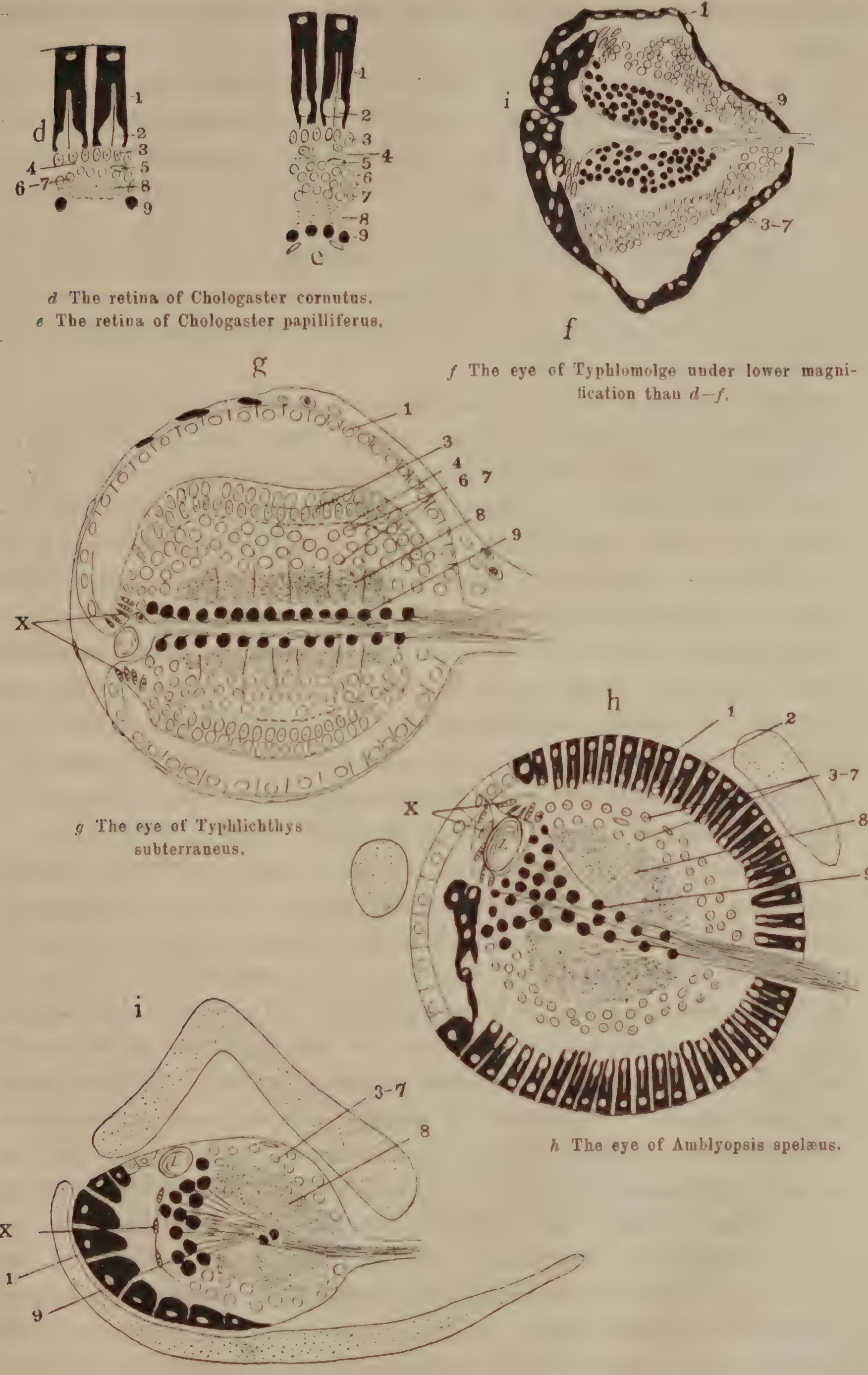
The most highly developed eye is that of Chologaster papilliferus. The parts of this eye are well proportioned, but the eye as a whole is small, measuring less than one millimeter in a specimen 55 mm long. The proportions of this eye are symmetrically reduced if it has been derived from a fish eye of the average size. The retina is much simpler than in Zygonectes. The simplifications in the retina have taken place between the outer nuclear and the ganglionic layers. The pigment layer has not been materially affected.

These facts are exactly opposed to the supposition of Kohl that the retina and the optic nerve are the last to be affected, and that the vitreous body and the lens cease to develop early. In Chologaster papilliferus (*b*) the latter parts are normal, while the retina is simplified. That the retina is affected first is proved beyond cavil by cornutus (*a*). The vitreous body and the lens are here larger than in papilliferus, but the retina is very greatly simplified. Cornutus, it must be borne in mind, lives in the open. The eye of Chologaster agassizii (*c*) differs from that of papilliferus largely in size. There is little difference in the retinas except the pigmented layer, which is about $26\,^0/_0$ thinner in agassizii than in papilliferus.

If we bear in mind that no two of the eyes represented here are members of a phyletic series, we may be permitted to state that from an eye like that of cornutus, but possessing scleral cartilages, both the eyes of Amblyopsis, and Troglichthys have been derived, and that the eye of Amblyopsis represents one of the stages through which the eye of Troglichthys passed. The eye of Amblyopsis (*h*) is the eye of C. cornutus minus a vitreus body with the pupil closed and with a minute lens. The nuclear layers have gone a step further in their degeneration than in cornutus, but



a to *c* are the eyes of Chologaster cornutus, papilliferus and agassizii, drawn to scale.



d The retina of Chologaster cornutus.
e The retina of Chologaster papilliferus.

f The eye of Typhlomolge under lower magnification than *d–f*.

g The eye of Typhlichthys subterraneus.

h The eye of Amblyopsis spelæus.

i The eye of Troglichthys rosae.

a to *i*. Diagramms of the eyes of all the species of the Amblyopsidae and of Typhlomolge, *d*, *e*, *g*, *h* and *i* are drawn under the same magnification.

the greatest modification has taken place in the dioptric arrangements.

In Troglichthys (*i*) even the mass of ganglionic cells present in the center of the eye as the result of the collapsing after the removal of the vitreous body has vanished. The pigmented epithelium, and in fact all the other layers, are represented by mere fragments.

The eye of Typhlichthys (*g*) has degenerated along a different line. There is an almost total loss of the lens and vitreous body in an eye like that of papilliferus without an intervening stage like that of cornutus, and the pigment layer has lost its pigment, whereas in Amblyopsis it was retained.

The reduction in size from the normal fish eye went hand in hand with the simplification of the retina. There was at first chiefly a reduction in the number of many times duplicated parts. Even after the condition in Chologaster papilliferus was reached the degeneration in the histological condition of the elements did not keep pace with the reduction in number (vide the eye of cornutus). The dioptric apparatus disappeared rather suddenly and the eye, as a consequence, collapsed with equal suddenness in those members which, long ago, took up their abode in total darkness. The eye not only collapsed, but the number of elements decreased very much. The reduction was in the horizontally repeated elements. The vertical complexity, on which the function of the retina really depends, was not greatly modified at first.

In those species which took up their abode in total darkness the degeneration in the dioptric apparatus was out of proportion to the degeneration of the retina, while in those remaining above ground the retinal structures degenerated out of proportion to the changes in the dioptric apparatus, which, according to this view, degenerates only under conditions of total disuse or total darkness which would necessitate total disuse. This view is upheld by the conditions found in Typhlogobius, as Ritter's drawings and my own preparations show. In Typhlogobius the eye is functional in the young and remains a light-perceiving organ throughout life. The fish live under rocks between tide water (Eigenmann '90). We have here an eye in a condition of partial use and the lens is not affected. The retina has, on the other hand, been horizontally reduced much more than in the Amblyopsidae, so that should the lens disappear, and Ritter found one specimen in which it was gone, the type of eye found in Troglichthys would be reached without passing through a stage found in Amblyopsis; it would be simply a horizontal contracting of the retina, not a collapsing of the entire eye.

The question may with propriety be asked here: Do the most degenerate eyes approach the condition of the pineal eye? It must be answered negatively.

2. Results of the Phyletic degeneration on the different parts of the eye.

The different structures of the eye may now be taken up in detail.

a) The eye muscles are normally developed in Chologaster. They are present to a greater or less extent in Amblyopsis. They have been reduced in number in Troglichthys, where the half nearest the eye has been replaced by bundles of fibrous tissue. In Typhlichthys they have vanished.

b) The scleras of the different members are not comparable on account of the presence of cartilage in some species and not in others. Both this layer and the choroid are insignificant in Chologaster and Typhlichthys. In Amblyopsis cartilages different in size and number are found anywhere about the eye, being frequently present in shape and position to suggest a displaced lens. In thickness the cartilages are disproportionate to the size of the eye. In Troglichthys we have a still more evident misfit, for the scleral cartilages are both too long and too thick. Evidently the scleral cartilages have not decreased in size in the same ratio as the eye.

c) The choroid is thin in all cases except where pigment cells are situated. These are frequently several times as thick as the rest of the choroid. In Amblyopsis the pigmentation of the choroid is inversely proportional to the pigmentation of the retina.

d) The lens has already received sufficient attention. It is merely necessary to insist again that as long as an eye is functional to any extent, the lens — in fact the dioptric apparatus in general — does not degenerate and that when absolute disuse comes the lens both phylo- and ontogenetically disappears rapidly. In Typhlogobius Ritter found the lens absent in one very old individual, and Cope found that in Gronias the lens is sometimes present on one side, while not on the other. In Amblyopsis and Typhlichthys it has degenerated to a mere vestige, or is gone altogether. Ritter, after considering the structure of degenerate eyes as far as known at the time, came to the conclusion »that the lens disappears before the retina; and that, where degeneration takes place at all in ontogeny, the lens is affected first and most profoundly«. With the first part of this statement the more recent observations are in full accord. It is, however, doubtful whether the lens is ever the first part affected; in fact the retina always leads, but certainly the lens, if affected at all, is affected profoundly.

e) There is more variety in the degree of development of the pigment epithelium than in any other structure of the eye. Ritter has found that in Typhlogobius this »layer has actually increased in thickness concomitantly with the retardation in the development of the eye, or it is quite possible with the degeneration of this particular part of it. An increase of pigment is an incident to the gradual diminution in functional importance and structural completeness«. There is so much variation in the thickness of this layer in various fishes that not much stress can be laid on the absolute or relative thickness of the pigment in any one species as an index of degeneration. While the pigment layer is, relative to the rest of the retina, very thick in the species of Chologaster, it is found that the pigment layer of Chologaster is not much if any thicker than that of Zygonectes, exception must be made for specimens of the extreme size in papilliferus and agassizii. In other words, primarily the pigment layer has retained its normal condition, while the rest of the retina has been simplified, and there may even be an increase in the thickness of the layer as one of its ontogenetic modifications. Whether the greater thickness of the pigment in the old Chologaster is due to degeneration or the greater length of the cones in a twilight species I am unable to say. In Typhlichthys, which is undoubtedly derived from a Chologaster-like ancestor, no pigment is developed, the layer retains its epithelial nature and remains apparently in its embryonic condition. It may be well to call attention here to the fact that the cones are very sparingly developed, if at all, in this species. In Amblyopsis, in which the degeneration of the retina has gone further, but in which the cones are still well developed, the pigment layer is very highly developed, but not by any means uniformly so in different individuals. The pigment layer reaches its greatest point of reduction in rosae, where pigment is still developed, but the layer is fragmentary except over the distal part of the eye. We thus find a development of pigment with an imperfect layer in one case and a full developed layer without pigment in another Typhlichthys. In the Chologasters the pigment is prismatic; in the other species granular. The rods disappear before the cones.

f) In the outer nuclear layer a complete series of steps is observable from the two-layered condition in papilliferus to the one-layered in cornutus, to the undefined layer in Typhlichthys and the merging of the nuclear layer in Amblyopsis, and their occasional total absence in rosae. The rods disappear first, the cones long before their nuclei.

g) The outer reticular layer naturally meets with the same fate as the outer nuclear layer. It is well developed in papilliferus and agassizii, evident in C. cornutus, developed in spots in Typhlichthys, and no longer distinguishable in the other species.

h) The layers of horizontal cells are represented in papilliferus by occasional cells; they are rarer in cornutus and beyond these have not been determined with certaints.

i) The inner nuclear layer of bipolar and spongioblastic cells is well developed in papilliferus and agassizii. In cornutus it is better developed in the young than in the older stages, where it forms but a single layer of cells. There is evidently in this species an ontogenic simplification. In the remaining species it is, as mentioned above, merged with the outer nuclear layer into one layer which is occasionally absent in Troglichthys.

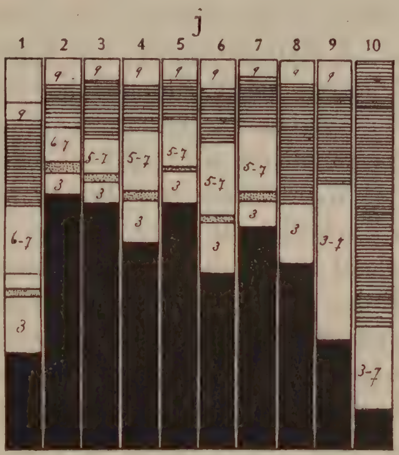


Diagram showing the percents of the total thickness of each of the layers of the retina in 1 Zygonectes notatus. 2 Chologaster cornutus 27 mm long. 3 43 mm long. 4 Chologaster papilliferus 29—39 mm and 5 55 mm long. 6 Chologaster agassizii 38 mm long and 7 62 mm long. 8 Amblyopsis. 9 Typhlichthys. 10 Troglichthys.

j) The inner reticular layer is relatively better developed than any of the other layers, and the conclusion naturally forces itself upon one that it must contain other elements besides fibers of the bipolar and ganglionic cells, for, in Amblyopsis and Troglichthys, where the latter are very limited or absent, this layer is still well developed. Horizontal cells have only been found in the species of Chologaster.

k) In the ganglionic layer we find again a complete series of steps from the most perfect eye to the condition found in Troglichthys. In papilliferus and agassizii the cells form a complete layer one cell deep except where they have given way to the optic fiber tracts which pass in among the cells instead of over them. In cornutus the cells have been so reduced in number that they are widely separated from each other. With the loss of the vitreous cavity the cells have been brought together again into a continuous layer in Typhlichthys, although there are much fewer cells than in cornutus even. The next step is the formation of a solid core of ganglionic cells, and the final step the elimination of this central core in Troglichthys, leaving but a few cells over the anterior face of the retina.

l) Müllerian nuclei are found in all but Amblyopsis and Troglichthys. In Ch. cornutus they lie in part in the inner reticular and the ganglionic layer. Cells of this sort are probably also found among the ganglionic cells of Typhlichthys.

We thus see that the simplification or reduction in the eye is not a horizontal process. The purely supporting structures like the scleral cartilages have been retained out of all proportion to the rest of the eye. The pigment layer has been both quantitatively and qualitatively differently affected in different species. There was primarily an increase in the thickness of this layer, and later a tendency to total loss of pigment. The degeneration has been more uniformly progressive in all the layers within the pigment layer. The only possible exception being the inner reticular layer, which probably owes its retention more to its supporting than to its nervous elements. Another exception is found in the cones, but their degree of development is evidently associated with the degree of development of the pigmented layer. As long as the cones are developed the pigmented layer is well developed or vice versa.

3. Ontogenic degeneration.

The developmental side of this question will be taken up with the development of the eye im Amblyopsis.

The simplification of the eye in cornutus has been mentioned in the foregoing parapraphs. It may be recalled that the nuclear layers are thinner in the old than in the young. There is here not so much an elimination or destruction of element as a simplification of the arrangements of parts, comparatively few being present to start with.

The steps in ontogenic degeneration can not be given with any degree of finality for Amblyopsis on account of the great variability of the eye in the adult. While the eyes of the very old have unquestionably degenerated there is no means of determining what the exact condition of a given eye was at its prime. In the largest individual examined the eye was on one side a mere jumble of scarcely distinguishable cells, the pigment cells and scleral cartilages being the only things that would permit its recognition as an eye. On the other side the degree of development was better. The scleral cartilages are not affected by the degenerative processes and are the only structures that are not so affected. The fact that the eyes are undergoing ontogenic degeneration may be taken, as suggested by Kohl, that these eyes have not yet reached a condition of equilibrium with their environment or the demands made upon them by use. Furthermore the result of the ontogenic degeneration is a type of structure below anything found in phylogeny. It is not so much a reduction of the individual parts as it is a wiping out of all parts.

4. Plan and process of Phyletic degeneration.

Does degeneration follow the reverse order of development or does it follow new lines, and if so, what determines these lines? Since the ontogenic development of the eye is supposed to follow in general lines its phyletic development the above question resolves itself into whether or no the eye is arrested at a certain stage of its morphogenic development, and whether this causes certain organs to be cut off from development altogether. In this sense the question has been answered in the affirmative by Kohl. Ritter, while unable to come to a definite conclusion, notes the fact that in one individual of Typhlogobius the lens which is phyletically a new structure had disappeared. This lens had probably been removed as the result of degeneration rather than through the lack of development. Kohl supposes that in animals placed in a condition where light was shut off more or less every succeeding generation developed its eye less. Total absence of light must finally prevent the entire anlage of the eye. Time has not been long enough to accomplish this in any vertebrate. Phyletic degeneration is looked upon as the result of a long series of Hemmungen which in successive generations appeared in ever earlier time of ontogenic development in always lower stages of the development of the individual eyes. The eye develops after the vertebrate type. At certain stages the rate of progress is diminished and in most cases finally completely ceases. A Hemmung has developed that in a shorter or longer period during which the development, is ever becoming slower, ends in the cessation of all development. The first appearance of the retardation falls in a time of embryonic or postembryonic development that in the phylogeny corresponds to the moment when the lack of light became operative. The period in ontogeny which lies between the first disturbance in development and its cessation corresponds to the phyletic time during which the development of the eye is checked at a continually lower stage of development. The point of cessation in ontogeny corresponds to the time when the eye reached its equilibrium. If in ontogeny there is undoubted degeneration, it is always an indication that the eye has not yet reached the point where it is in equilibrium with its functional requirements; in other words degeneration leads to further retardation. On the very next page we are told degeneration is a consequence of retardation. Degeneration is the means of obtaining developmental cessation. The organs have reached a stage of developmental cessation and are undergoing degeneration. The first is a condition caused by the second which is a process. In most cases the Hemmung is simply a stopping at a certain stage of development. The parts of the eye continue to differentiate for a time, as long as the greatly decreased and final cessation of addition of material permits. The cessation of development does not take place at the same time in all parts of the eye. The less important, those not essential to the perception of light, are disturbed first. The retina and the optic nerve are the last affected, the iris comes next in the series. Because the cornea, aqueous and vitreous bodies and the lens are not essential for the performance of the function of the eye these structures cease to develop early. The processes of degeneration follow the same rate. Degeneration is brought about by the falling apart of the elements as the result of the introduction of connective tissue cells that act as wedges. Abnormal degeneration sometimes becomes manifest through the cessation of the reduction of parts (page 269) that normally decrease in size so that these parts in the degenerate organ are unusually large.

Kohl's theoretical explanation here given somewhat at length is based on the study of an extensive series of degenerate eyes. He has not been able to test the theory in a series of animals living actually in the condition he supposes for them, and has permitted his erroneous interpretation of the highly degenerate eye of Troglichthys to lead him to this theory of the arresting of the eye in ever earlier stages of ontogeny. It has been shown in previous pages that this most degenerate eye is in an entirely different condition from that supposed by him. The mere checking of the normal morphogenic development has done absolutely nothing to bring about this condition, and it could not have been produced by the checking of development in ever earlier and earlier stages of ontogeny, for there is no stage in normal ontogeny resembling in the remotest degree the eye of Troglichthys. The process of degeneration as seen in the Amblyopsidae is in the first instance one of growing smaller and simpler — not a cutting off of late stages in the development. The simplified condition, it is true, appears earlier and earlier in ontogeny till it appears along the entire line of development, even in the earliest stages. But the tendency for characters added at the end of ontogeny to appear earlier and earlier in the ontogeny is well known, and there is no inherent reason why an organ disappearing in the adult should not eventually disappear entirely from ontogeny. The fact that organs which have disappeared in the adult have in many instances not also disappeared in the ontogeny and remain as so-called rudimentary organs has received an explanation from SEDGWICK. In his re-examination of the biogenetic law he came to the conclusion that »the only functionless ancestral structures, which are present in development, are those which at some time or another have been of use to the organism during its development after they have ceased to be so in the adult«. All organs functionless in the adult but functional in the early ontogeny develop in the normal way. Organs no longer functional at any time dwindle all along the line of development. In Typhlogobius, where the eye is functional in the young, it develops in full size in the embryo and it is not till late in life that degeneration is noticeable. In Amblyopsis on the other hand, where the eye has not been functional at any period of ontogeny for many generations, where degeneration begins at an early period and continues till death, the degenerate condition has reached the early stages of the embryo. It is only during the first hour or so that the eye gives promise of becoming anything more than it eventually does become. The degree of degeneration of an organ can be measured as readily by the stage of ontogeny when the degeneration becomes noticeable as by the structure in the adult. The greater the degeneration, the further back in the ontogeny, the degenerate condition becomes apparent unless, as stated above, the organ is of use at some time in ontogeny. It is evident that an organ in the process of being perfected by selection may be crowded into the early stages of ontogeny by post selection. Evidently the degenerate condition is not crowded back for the same reason. How it is crowded back I am unable to say. A satisfactory explanation of this will also be a satisfactory explanation of the process by which individually acquired characteristics are enabled to appear in the next generation. The facts, which are patent, have been formulated by HYATT in his law of tachygenesis. HYATT '89, page IX.

Cessation of development takes place only in so far as the number of cells are concerned. The number of cell-generations produced being continually smaller result in an organ as a consequence, also smaller. In this sense we have a cessation of development (cell division, not morphogenic development) in ever earlier stages. That there is an actual retardation of development is evident from Amblyopsis and Typhlichthys in which the eye has not reached its final form when the fish are 35 mm long.

Histogenic development is a prolonged process, and ontogenic degeneration is still operative at least in Amblyopsis.

Degeneration is not the result of the ingrowth of connective tissue cells as far as I can determine. It is rather a process of starving, of shriveling or resorbtion of parts.

From the foregoing it is evident that degeneration has not proceeded in the reverse order of development, rather the older normal stages of ontogenic development have been modified into the more recent phyletic stages through which the eye has passed. The adult degenerate eye is not an arrested ontogenic stage of development, but a new adaptation, and there is an attempt in ontogeny to reach the degenerate adult condition in the most direct way possible.

5. The Causes of Individual and Phyletic Degeneration.

It may now be profitable to take up the causes leading to the small degree of degeneration found in Chologaster, the degeneration of the eye in Amblyopsis, Typhlichthys and Troglichthys to a mere vestige together with the total disappearance of some of the accessory structures of the eye as the muscles. In the outset of this consideration we must guard against the almost universal supposition that animals depending on their eyes for food are or have been colonizing caves, or that the blind forms are the results of catastrophies that have happened to eyed forms depending on their eyesight for their existence. This idea, so prevalent, vitiates nearly everything that has been written on the degeneration of the eyes of cave animals[1]).

The degeneration of organs ontogenically and phylogenically has received a variety of explanations.

1. The organ diminishes with disuse (ontogenic degeneration LAMARCK, ROUX, PACKARD) and the effect of this disuse appears to some extent in the next generation (phylogenic degeneration LAMARCK, ROUX, PACKARD).

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[1]) Most of the speculations on the origin of blind forms have been based solely on their structure without considering either the habits or locations of the species. Practically all we know of the habits of the blind forms is from speculations based on their mummies.

KOHL, without any basis of facts other than the results obtained from sections, supposes that the eye did not begin to degenerate until the developmental energy that vent to build the eye began to go to the development of the compensating structures after the species got into the dark.

The fact that four out of six species of a family of fishes should be found adapted to an underground existence, the further fact that all four of these are of distinct origin, and furthermore that they are not all found in the same regions, with the additional fact that while many other species of fishes are found in these caves no other species of the varied fauna in the epigean streams about the caves have become adapted to an underground existence, is proof positive that the Amblyopsidae do not owe their underground existence to sudden or accidental causes.

The habits of Chologaster papilliferus and Amblyopsis furnish the key to the situation. Papilliferus is negatively heliotropic.

Through the efforts of Mr. E. B. FORBES I obtained a school of 30 specimens of this species, some of which I kept in aquaria over a year. An account of the observations made on this school will be published elsewhere.

It hides under rocks and in all sorts of dark corners, and though provided with more highly developed eyes than any other species of the family procures its food by means of its highly developed tactile organs. Amblyopsis has retained its negatively heliotropic character with a total absence of functional eyes, and both it and Typhlichthys have retained their habit of hiding under stones and under ledges of rocks in the underground streams where light never penetrates. The tactile apparatus, so highly developed in the blind species, did not receive their initial high differentiation as a compensation for the loss of the eyes. On the contrary the eyes were lost as the indirect result of the high development of the tactile organs.

Which enabled the species to maintain themselves during their exploration and colonization of the underground streams.

This question will be fully dealt with elsewhere.

2. Through a condition of panmixia the general average maintained by selection is reduced to the birth mean in one generation (ontogenic ROMANES, LANKESTER, LLOYD MORGAN, WEISMANN) to the greatest possible degeneration in succeeding generations (phylogenic WEISMANN), or but little below the birth average of the first generation (WEISMANN'S later view, ROMANES, MORGAN, LANKESTER).

3. Through natural selection (reversed) the struggle of persons the organ may be caused to degenerate either (*A*) by the migration of persons with highly developed eyes from the colony living in the dark (LANKESTER), or (*B*) through economy of weight and nutriment or liability to injury (phylogenic purely, DARWIN, ROMANES).

4. Through the struggle of parts (*a*) for room an unused organ in the individual may be crowded (ontogenic ROUX), (*b*) for food, this may lead to the development of the used organ as against the disused through a compensation of growth (GOETHE, ST. HILAIR, ROUX), this ontogenic result becomes phylogenic through transmission of the acquired character (ROUX), or is in its very nature phyloblastic (KOHL).

5. Through the struggle between soma and germ to produce the maximum efficiency of the former with the minimum expenditure of the latter (onto- and phylogenic LENDENFELD).

6. Through germinal selection, the struggle of the representatives of organs in the germ (onto- and phylogenic WEISMANN).

The idea of ontogenic degeneration is intimately bound up with the idea of phylogenic degeneration. Logically we ought to consider first the causes of individual degeneration, and then the processes or causes that led to the transmission of this. Practically it is impossible to do so, because many of the explanations are general. Only number 4 of the above may be taken in the ontogenic sense purely, though it was certainly also meant to explain phylogenic degeneration. In many of the explanations of particular cases of degeneration more than one of the above principles are invoked though only one was meant to be used. In most cases however the discussions of degeneration have been in general terms, without direct bearing on any specific instance of degeneration in all its details. It must be evident that such discussions can only by accident lead to right results.

By the Lamarckian ontogenic degeneration is considered the result of lack of use and consequent diminished blood supply. The results of the diminution caused by the lack of use during one generation are transmitted is some degree to the next generation which thus starts at a lower level. A continuation of the same conditions lead finally to the great reduction and ultimate disappearance of an organ.

No one, so far as I am aware, has attempted, or perhaps better, succeeded to account with this factor in detail for the degeneration of the eye. PACKARD's '94 explanations are evidently a mixture of Lamarckism and Darwinism.

PACKARD says, »When a number, few or many, of normal, seeing animals enter a totally dark cave or stream, some may become blind sooner than others«, some having the eye slightly modified by disuse, while others may have in addition physical or functional defects especially in the optic nerves and ganglia. »The result of the union of such individuals and of adaptation to their stygian life would be broods of young, some with vision unimpaired, others with a tendency to blindness, while in others there would be noticed the first steps in degeneration of nervous power and nervous tissue.« PACKARD evidently had invertebrates in mind. He clearly admits the cessation of selection or panmixia in that those born with defects may breed with the others. He supposes that the blind fauna may have arisen in but few or several generations, a supposition that may be applicable to invertebrates, but certainly is not to the vertebrates. At first those becoming so modified that they can do without the use of their eyes would greatly preponderate over those »congenitally blind«. »So all the while the process of adaptation going on, the antennae and other tactile organs increasing in length and in the delicacy of structures, while the eyes were meanwhile diminishing in strength of vision and their nervous force giving out, after a few generations perhaps only two or three the number of congenitally blind would increase, and, eventually they would, in their turn, preponderate in numbers.« PACKARD seems here to admit the principle of degeneration as the result of compensation of growth, the nervous force of the eye giving out with the increase of the tactile and olfactory organs. It is somewhat doubtful in what sense the term »congenitally blind« is used, but it probably means born blind as the result of transmitted disuse rather than blind as the result of fortuitous variation. The effects of disuse are thus supposed through their transmission to have given rise to generations of blind animals. The continued degeneration is not discussed.

In 1873, 1874 and 1890 ROMANES in a series of articles in

Nature and later in DARWIN and after DARWIN II, page 291 et seq. maintained that the beginning of degeneration is due to cessation of selection, and continued degeneration to the reversal of selection and final failing of the power of heredity. Selection he supposed to be reversed because the organ no longer of use »is absorbing nutriment, causing weight, occupying space, and so on, uselessly. Hence even if it be not also a source of actual danger, economy of growth will determine a reversal of selection against an organ which is now not only useless, but deleterious«. This process will continue until the organ has reached »so minute a size that its presence is no longer a source of detriment to the organism, the cessation of selection will carry the reduction a small degree further; and then the organ will remain as a ‚rudiment'«. Since however we can not consider that the force of heredity is everlasting, it will eventually fail and the organ dwindle still further and disappear. This failure of heredity MORGAN (Animal Life page 793) is unable to distinguish from the effect of disuse without which »the reduction of organs is difficult to explain«.

The principles involved in this explanation are panmixia, natural selection, and, according to MORGAN, disuse transmission.

WEISMANN, Nature, 1886 and Essays, vol. II, 1, contended that cessation alone, or panmixia as he terms it, is sufficient to account for all degeneration. He later gave up this view for his theory of germinal selection, of which more later.

ROUX starting with the then generally accepted view that acquired characters are transmitted, attempted chiefly to explain degeneration in the individual. Degeneration is looked upon as the result of a struggle among the parts for a) room and b) food. He emphasizes the fact that a reduced functional activity continued for a long period reduces the functional possibility of an organ (page 176). The diminished use not only brings about this simple atrophy, but also the reduction, by stronger neighbors, to such a volume as is still of advantage to the animal. Disused organs that are not in the struggle for room may maintain themselves a long time. The struggle among parts for food, which implies the principle of compensation of growth of GOETHE, need not take place through the withdrawal of blood, but may take place through the more active osmotic selection by the stronger organ of food that would otherwise go to the weaker.

Without doubting that both these principles are active agents in degeneration it may be seriously doubted whether they were effective in the degeneration of the eyes in question. Certainly there can be no question of a struggle for room, for the position and room formerly occupied by the eye is now filled with fat which can not have been operative against the eye. The presence of this large fat mass in the former location of the eye, the large reserve fat mass in the body, the uniformly good condition of the fish and the low vitality which enables them to live for months without visible food all argue against the possibility that the struggle for food between parts was an active agent in the degeneration of the eyes.

Kohl considers that »Der Grund, und direkter oder indirekter Anlass zum Eintreten der Entwickelungshemmung ist Lichtmangel«. The method of the direct operation of the lack of light he conceived to be as follows:

The ancestry of blind animals lived where the light was uninterrupted and they had developed eyes. They got into an environment where the light was shut off more or less. The first generations retained their fully developed eyes without, however, being able to put them to full use. In consequence during phylogeny other organs became highly developed to compensate for the disuse of the eye. (Through natural selection?) Thus touch organs (Myxine, Siphonops) or the auditory organs (Talpa and possibly Typhlichthys) became more highly developed. The eye was unnecessarily highly developed. A process of degeneration (Rückbildung) began, which was never very extensive. Much more potent in placing the eye in harmony with its environment was the fact that every succeeding generation developed its eye less. This process of Hemmung of the eye did not begin until the developmental force began to go to the development of the compensating organs. On account of the loss of this developmental force the eye was unable to reach, in successive generations, the former grade. The degeneration is thus explained as the result of a struggle of parts, although this term is nowhere used, acting through the principle of compensation. The same objections may be offered to this explanation of Kohl as to all his theoretical discussions; they are based on the assumption of conditions and processes that have no existence. The high development of »compensating« organs is not primarily the result of the loss of the eye, but the high development of the latter organs permitted the disuse and later degeneration of the former. His whole process is a phylogenic one without a proceeding ontogenic one, though on this point he does not seem to be very clear himself, for, on one page we are told that degeneration leads to retardation, and on another that degeneration is a consequence of retardation.

Lendenfeld, '96, endeavors to apply Roux's Kampf der Theile with reversed selection to explain the conclusions reached by Kohl on the processes and causes of degeneration. The struggle is represented to take place between the germ and soma, the former endeavoring to keep the latter at the lowest efficient point as weapon for the germ. If a series of individuals gets into the dark, the organs of vision are of no advantage, and reversed selection will bring about their degeneration. The saving in ontogeny appears first as a retardation and then a cessation of development.

Weismann, more recently accepts the view of Romanes, Morgan and Lankester of the inadequacy of panmixia to explain the whole phenomena of degeneration, and in his Germinal Selection '96 rejects the indea of reversed selection and suggests a new explanation for what Romanes attributed to the failure of heredity and the Lamarckian's to disuse transmission. The struggle of the parts of Roux has been crowded by him back to the representatives of these parts in the germ.

»The phenomena observed in the stunting, or degeneration, of parts rendered useless show distinctly that ordinary selection, which operates by the removal of entire persons, personal selection, as I prefer to call it, cannot be the only cause of degeneration; for in the most cases of degeneration it can not be assumed that slight individual vacillations in the size of the organ in question has possessed selective value. On the contrary, we see such retrogressions affected apparently in the shape of a continuous evolutionary process determined by internal causes, in the case of which there can be no question whatever of selection of persons or of a survival of the fittest that is of individuals with the smallest rudiments.« The gradual diminution continuing for thousands and thousands of years and culminating in its final and absolute effacement can only be accomplished by germinal selection. Germinal selection as applied to degeneration is the formal explanation of Romanes' failure of the hereditary force and the establishment of disuse effects in the heredity through the struggle of parts for food. »Powerful determinants will absorb nutriment more rapidly than weaker determinants. The latter, accordingly, will grow more slowly and will produce weaker determinants than the former.« If an organ is rendered useless, the size of this organ is no longer an element in personal selection. This alone would result in a slight degeneration. Minus variations are, however, supposed to rest »on the weaker determinants of the germ, such as absorb nutriment less powerfully than the rest. This will enable the stronger determinants to deprive them even of the full quantum of food corresponding to their weakened capacity of assimilation and their descendants will be weakened still more. Inasmuch now, as no weeding out of the weaker determinants of the hind leg (eye) by personal selection takes place on our hypothesis, inevitably the average strength of this determinant must slowly but constantly diminish, that is, the hind leg (eye) must grow smaller and smaller until it finally disappears altogether«. »Panmixia is the indispensable precondition of the whole process; for owing to the fact that persons with weak determinants are just as capable of life as those with strong, solely by this means is a further weakening effected in the following generations.«

This theory presupposes the complex structure of the germplasm formulated by WEISMANN and rejected by various persons for various reasons[1]). But granting WEISMANN the necessary structure of the germplasm, can germinal selection accomplish what is claimed for it? I think not. Granting that variation occurs about a mean would not all the effects claimed for minus variations be counteracted by positive variations. Eye determinants that on account of their strength secure more than their fair share of food and thereby produce eyes that are as far above the mean as the others are below may leave descendent determinants that are still stronger than their ancestry. It is evident that a large, really extravagant development of the eye in such a fish as Chologaster would not effect the removal of the individual by personal selection, still less so in Amblyopsis which not only lives in comparative abundance, but has lived for 20 months in confinement without visible food. It seems that all the admitted objections to degeneration by panmixia apply with equal force to germinal selection. This however would be changed were the effect of disuse admitted to affect the determinants, and this it seems WEISMANN has unconsciously admitted. So far we have considered germinal selection in the abstract only. All its suppositions are found to be but a house of cards when the actual conditions of degeneration are considered. We find that degeneration is not a horizontal process affecting all the parts of an organ alike as Weismann presupposes, not even a process in the reverse order of phyletic development, but the more vital, most worked parts degenerate first with disuse and panmixia, the passive structures remain longest. The rate of degeneration is proportional to the past activity of the parts and the statement that »passively functioning parts, that is, parts which are not alterable during the individual life by function, by the same laws also degenerate when they become useless« finds no basis in fact and is an example of the inexact utterances abundant in the discussion of degeneration, on which it is entirely unsafe to build lofty theoretical structures. As one example of the unequal degeneration we need only call attention to the scleral cartilages and the rest of the eye of Troglichthys rosae.

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[1]) My own objections are based on the study of the reproductive organs of the viviparous fish, Cymatogaster. '96.

All are agreed that natural selection alone is insufficient to explain all, if any, of the processes of degeneration. All either consciously or not admit the principle of panmixia, and all are now agreed that this process alone can not produce extensive degeneration. All are agreed that the important point is, degeneration beyond the point reached by panmixia, the establishment of the degenerating process whatever it may be in the germ, or in other words the breaking of the power of heredity. It is in the explanation of the latter that important differences of opinion exist.

Weismann attempts to explain the degeneration beyond the point which panmixia can reach by a process which not only is insufficient if all his premises are granted to produce the desired result without the help of use transmission, but has as its result a horizontal degeneration which has no existence in fact.

Romanes supposed degeneration, beyond the point which may be reached by panmixia, to be the result of personal selection and the failure of the hereditary force. The former is not applicable to the species in question and is denied by such an ardent Darwinian as Weismann to be applicable at all in accounting for degeneration. Moreover the process as explained by Romanes would result in a horizontal degeneration which has no existence in fact. The second assumption, the failure of hereditary force, is not distinguishable, as Morgan has pointed out, from the effect of use transmission.

The struggle of parts in the organism has not affected the eye through the lack of room since the space formerly occupied by the eye is now filled by fat and not by an actively functioning organ. It is not affected by the struggle for food, for stored food occupies the former eye space. It could only be affected by the more active selection of specific parts of food by some actively functioning organ. It is possible that this has in fact affected the degeneration of the eye. The theory explains degeneration in the individual and implies that the effect in the individual should be transmitted to the next generation. This second fact seems but the explanation of the working of the Lamarckian factor.

The Lamarckian view, that through disuse the organ is diminished during the life of the individual, in part at least on account of the diminution of the amount of blood going to a resting organ and that this effect is transmitted to succeeding generations, not only would theoretically account for unlimited progressive degeneration, but is the only view so far examined that does not on the face of it present serious objections. Is this theory applicable in detail to the conditions found in the Amblyopsidae? Before going further, objections may be raised against the universal assumption that the cessation of use and the consequent panmixia was a sudden process. This assumes that the caves were peopled by a catastrophy. But it is absolutely certain that the caves were not so peopled, that the cessation of use was gradual, and the cessation of selection must also have been a gradual process. There must have been ever widening bounds within which the variation of the eye would not subject the possessor to elimination.

Chologaster is in a stage of panmixia as far as the eye is concerned. It is true the eye is still functional, but that the fish can do without its use is evident by its general habit and by the fact that it sometimes lives in caves.

The present conditions have apparently existed for countless generations, as long as the present habits have existed, and yet the eye still maintains a higher degree of structure than reversed selection, if operative, would lead us to expect, and a lower than the birth mean of fishes depending on their eyes, the condition that the state of panmixia alone would lead us to expect. There is a staying quality about the eye with the degeneration, and this can only be explained by the degree of use to which the eye is subjected.

The results in Chologaster are due to Panmixia and the limited degree of use to which the eye is put. Chologaster agassizii shows the rapid diminution of the eye with total disuse.

The difference in the conditions between Chologaster and Amblyopsis, Typhlichtys and Troglichthys is that in the former the eyes are still in use, except when living in caves; in the latter they have not been in a position to be used for hundreds of generations. The transition between conditions of possible use and absolute disuse may have been rapid with each individual after permanently entering a cave. Panmixia as regards the minute eye continued. Reversed selection, for economy can not have affected the eye for reasons already stated. Simply the loss of the force of heredity, unless this was caused by disuse, or the process of germinal selection can not have brought about the conditions, because some parts have been affected more than others.

Considering the parts most affected and the parts least affected the degree of use is the only cause capable of explaining the conditions. Those parts most active during use are the ones reduced most, viz., the muscles, the retina, optic nerve and dioptric appliances, the lens and vitreous parts. Those organs occupying a more passive position, the scleral cartilages, have been much less affected and the bony orbit least. The lens is one of the latest organs affected, not at all during use, possibly because during use it would continually be in use. It disappears most rapidly after the beginning of absolute disuse both onto- and phylogenetically. All indications point to use and disuse as the effective agent in moulding the eye. The process does however not give results with mathematical precision. In Typhlichthys subterraneus the pigmented layer is affected differently from that of Amblyopsis. The variable development of the eye muscles in different species would offer another objection if we did not know of the variable condition of these structures in different individuals. Chilton has objected to the application of the Lamarckian factor to explain degeneration on account of the variable effects of degeneration in various invertebrates. But such differences in the reaction are still less explicable by any of the other theories.

6. Summary.

1. There are at least six species of »blind-fishes«, Amblyopsidae inhabiting North America. Three with well developed eyes and three with mere vestiges.

2. The three species with vestigial eyes are descended from generically distinct ancestors with well developed eyes.

3. These species can be more readily distinguished by the structure of their eyes than by any other characteristic.

4. The most highly developed eye is much smaller and simpler than the eye of normal-eyed fishes.

5. The structure of their eyes may be represented by the following key to the genera and species:

a) Vitreous body and lens normal, the eye functional. No scleral cartilages. Eye permanently connected with the brain by the optic nerve. Eye muscles normal. No optic fibre layer. Minimum diameter of the eye 700 μ . . . . Chologaster.

b) Eye in adult more than 1 mm in longitudinal diameter. Lens over 0.5 mm in diameter. Retina very simple, its maximum thickness 83.5 μ in the old; the outer and inner nuclear layers consisting of a single series of cells each; the ganglionic layer of isolated cells. Maximum thickness of the outer nuclear layer 5 μ; of the inner layer 8 μ . . . . cornutus.

bb) Eye in adult less than 1 mm in longitudinal diameter. Lens less than 0.4 mm. Outer nuclear layer composed of at least two layers of cells; the inner nuclear layer of at least 3 layers of cells, the former at least 10 μ thick, the latter at least 18 μ.

c) Pigment epithelium 65 μ thick in the middle aged, 102 in the old . . . . papilliferus.

cc) Pigment 49 μ thick in the middle aged, 74 in the old; 24—30% thinner than in papilliferus. Eye smaller . . . . agassizii.

aa) The eye a vestige, not functional; vitreous body and lens mere vestiges; the eye collapsed, the inner faces of the retina in contact; maximum diameter of eye about 200 μ.

d) No scleral cartilages; no pigment in the pigment epithelium; a minute vitreal cavity; hyaloid membrane with blood vessels. Pupil not closed. Outer nuclear, outer reticular, inner nuclear, inner reticular, ganglionic and pigment epithelial layers differentiated. Cones probably none. No eye muscles. Maximum diameter of eye 180 μ. Eye probably connected with brain throughout life . . . . Typhlichthys.

dd) Scleral cartilages; pigment in the pigment epithelium; vitreal cavity obliterated; no hyaloid membrane. Pupil closed. Some of the eye muscles developed. No outer reticular layer. Outer and inner nuclear layers merged into one. Eye in adult not connected with the brain.

e) Pigment epithelium well developed; cones well developed; ganglionic cells forming a funnel-shaped mass through the center of the eye. Pigment epithelium over the front of the eye without pigment. Maximum diameter of eye about 200 μ . . . . Amblyopsis.

ee) Pigment epithelium developed on distal face of the eye, rarely over the sides and back. No cones. Nuclear layers mere vestiges; the ganglionic layer restricted to the anterior face of the eye just within the pigmented epithelium. Maximum diameter of eye about 85 μ . . . . Troglichthys.

6. The steps in degeneration are seen in diagrams *a* to *i*.

7. The structure of the vestigial eyes differs much in different individuals.

8. The eye of Chologaster is an eye symmetrically reduced from a larger normal fish eye.

9. The retina in Chologaster is the first structure that was simplified.

10. Later the lens, and especially the vitreous body, degenerated more rapidly than the retina.

11. The eye of Typhlichthys has degenerated along a different line from that of Amblyopsis, its pigmented epithelium having been most profoundly affected.

12. The eye muscles have disappeared in Typhlichthys.

13. Troglichthys shows that the steps in the degeneration of the muscles were in the direction of lengthening their attaching tendons, finally replacing the muscles with strands of connective fibres.

14. The scleral cartilages have not kept pace in their degeneration with the active structures of the eye.

15. The lens in the blind species is, for the most part, a small group of cells without fibres.

16. The proportional degeneration of the layers of the retina is shown in diagram *j*.

17. With advancing age the eye of Amblyopsis undergoes a distinct ontogenic degeneration from the mature structure.

18. The phyletic degeneration does not follow the reverse order of development. None of the adult degenerate eyes resemble stages of past (phyletic) adult conditions.

19. The degenerate eyes do not owe their structure to a cessation of development at any past ontogenetic stage, i. e. at any stage passed through in the development of a normal eye.

20. Cessation in development occurs only in the reduction of the number of cell generations produced to form the eye not in cessation of morphogenic processes.

21. In some cases (Typhlichthys) there is a retardation in the

rate of development, the permanent condition being reached later in life than is usual in fishes. (It is possible that the pigment of the pigment epithelium never comes to develop at all. It is, however, impossible to assert this until the embryos of this species are examined. It is possible that the pigment degenerates before the stages are reached that I have examined.)

22. The degenerate condition of the eye appears in the embryo. The crowding back has followed the law of tachygenesis.

23. The conditions in the eyes of the Amblyopsidae can only be explained as the result of the transmission of disuse effect.

Zusammenfassung.

1. Amerika hat wenigstens sechs Species von »Blindfischen« oder Amblyopsiden. Drei von denselben haben gut entwickelte, drei rudimentäre Augen.

2. Die drei Species mit rudimentären Augen stammen ab von drei verschiedenen Gattungen mit gut entwickelten Augen.

3. Diese Species können leichter unterschieden werden nach der Struktur ihrer Augen, als nach anderen Merkmalen.

4. Selbst das am höchsten entwickelte Auge ist viel kleiner und einfacher als das normale Auge der Fische.

5. Die Struktur der Augen kann am besten vorgestellt werden nach folgendem Schlüssel zu den verschiedenen Genera und Species:

a) Glaskörper und Linse normal, die Augen funktioniren. Kein Scleralknorpel. Das Auge ist mit dem Gehirn durch den N. opticus zeitlebens verbunden. Augenmuskeln normal. Kein Stratum von Opticusfasern. Der geringste Durchmesser des Auges 700 μ . . . . Chologaster.

aa) Rudimentäre, nicht funktionirende Augen. Glaskörper und Linse nur rudimentär. Das Auge kollabirt. Die Innenschichten der Retina im Kontakt. Maximaler Durchmesser des Auges ungefähr 200 μ.

b) Das Auge ist beim Erwachsenen im longitudinalen Durchmesser größer als 1 mm. Die Linse über 0,5 mm im Durchmesser. Retina sehr einfach gebaut, die größte Dicke 83,5 μ bei alten Thieren. Die äußere und innere Körnerschicht besteht aus einer einfachen Zellenreihe. Die Ganglienschicht wird von isolirten Zellen gebildet. Die größte Dicke der äußeren Körnerschicht beträgt 5 μ, die innere Körnerschicht 8 μ . . . . cornutus.

bb) Das Auge beim Erwachsenen ist im longitudinalen Durchmesser kleiner als 1 mm. Die Linse kleiner als 0,4 mm. Die äußere Körnerschicht ist zusammengesetzt aus wenigstens zwei Zellenschichten; die innere Körnerschicht aus drei Zellenschichten; die erstere ist 10 μ dick, letztere 18 μ.

c) Das Pigmentepithel ist 65 μ dick bei halb ausgewachsenen, 102 bei alten Thieren . . . . papilliferus.

cc) Pigment 49 μ dick bei halb ausgewachsenen Thieren, 74 bei alten Thieren. 24—30 $^0/_0$ dünner als bei papilliferus. Das Auge kleiner . . . . . . agassizii.

d) Kein Scleralknorpel; kein Pigment im Pigmentepithel; eine winzig kleine Glaskörperhöhle; die Hyaloidmembran mit Blutgefäßen. Die Pupille nicht

geschlossen. Die äußere Körnerzone, die äußere Reticularzone, die innere Körner- und innere Reticularzone, die Ganglienzellen und Pigmentepithelschicht differenzirt. Zapfen fehlen wahrscheinlich. Keine Augenmuskeln. Der größte Durchmesser des Auges 180 μ. Das Auge wahrscheinlich mit dem Gehirn während des ganzen Lebens verbunden . . . . Typhlichthys.

dd) Scleralknorpel; Pigment im Pigmentepithel; die Glaskörperhöhle obliterirt; keine Hyaloidmembran. Die Pupille geschlossen. Einige Augenmuskeln entwickelt. Keine äußere Reticularschicht. Äußere und innere Körnerzone verschmolzen. Das Auge beim Erwachsenen nicht mit dem Gehirn verbunden.

e) Pigmentepithel gut entwickelt; Zapfen wohl entwickelt; die Ganglienzellen bilden im Centrum des Auges einen Trichter (funnel-shaped). Das Pigmentepithel entbehrt im vorderen Abschnitte des Auges des Pigmentes. Der größte Durchmesser des Auges ungefähr 200 μ . . . . Amblyopsis.

ee) Das Pigmentepithel ist an der distalen Fläche des Auges entwickelt, spärlicher an den Seiten und im inneren Theil. Keine Zapfen. Die Körnerzonen sehr rudimentär. Die Ganglienzellenschicht findet sich nur an der vorderen Fläche des Auges hinter dem Pigmentepithel. Der größte Durchmesser des Auges ist ungefähr 85 μ . . . . Troglichthys.

6. Der Verlauf der Degeneration ist in Diagramm *a—i* veranschaulicht (pag. 586 und 587).

7. Die Struktur der rudimentären Augen differirt bei verschiedenen Individuen beträchtlich.

8. Das Auge von Chologaster kann auf »symmetrische« Reduktion eines größeren normalen Fischauges zurückgeführt werden.

9. Bei Chologaster wird zunächst die Retina vereinfacht.

10. Später degeneriren die Linse und insbesondere der Glaskörper rascher als die Retina.

11. Das Auge von Typhlichthys ist auf andere Weise degenerirt als bei Amblyopsis. Das Pigmentepithel ist viel stärker degenerirt.

12. Bei Typhlichthys sind die Augenmuskeln verschwunden.

13. Bei Troglichthys beginnt die Degeneration der Muskeln als eine Verkürzung und Verlängerung der zugehörigen Muskelsehne. Zuletzt erscheint der Muskel durch Bindegewebsfibrillen ersetzt.

14. Der Scleralknorpel nimmt nicht gleichen Theil an der Degeneration der aktiven Strukturen des Auges.

15. Die Linse der blinden Arten wird in den meisten Fällen nur repräsentirt durch eine kleine Gruppe von Zellen ohne Fasern.

16. Die verhältnismäßige Degeneration der Schichten der Retina ist im Diagramm *j* zu ersehen (pag. 591).

17. Das Auge von Amblyopsis erfährt mit zunehmendem Lebensalter eine ausgesprochene ontogenetische Degeneration.

18. Die phyletische Degeneration folgt nicht der durch die Entwickelung gegebenen Reihenfolge. Kein einziges degenerirtes Auge eines ausgewachsenen Thieres entspricht Stadien erwachsener Vorfahren.

19. Die Struktur der rudimentären Augen ist nicht die Folge einer Sistirung der Entwickelung auf irgend welchem vergangenen ontogenetischen Stadium, d. h. auf einem Stadium der Entwickelung eines normalen Auges.

20. Ein Stillstand in der Entwickelung ist nur in so fern kenntlich, als eine Reduktion in der Zahl der gebildeten Zellgenerationen eintritt, nicht aber ein Stillstand des morphogenetischen Processes selbst.

21. In einzelnen Fällen (Typhlichthys) tritt eine Verlangsamung der Entwickelung ein. Die bleibenden Verhältnisse werden später erreicht als gewöhnlich bei Fischen. (Vielleicht kommt das Pigment in manchen Fällen gar nicht erst zur Entwickelung; daraufhin werden Embryonen der bezüglichen Species zu untersuchen sein. Es ist aber auch möglich, dass das Pigment in jüngeren, noch nicht untersuchten Stadien schon degenerirt war.)

22. Die Degeneration des Auges zeigt sich schon beim Embryo. Der Eintritt der Degeneration im Embryo erfolgt nach dem Gesetze der Tachygenesis.

23. Das Verhalten der Augen bei den Amblyopsiden kann nur erklärt werden als Resultat von erblichen Übertragungen von Erfolgen des Nichtgebrauchs.

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Description of Figures.

Plates XI—XV.

All figures were drawn with the aid of the Abbe camera, usually the Zeiss apochromatic 2 mm objective and the No. 4 eye piece, rarely the 4 mm objective was found available. Occasionally the $^1/_{12}$ oil immersion of Bausch and Lomb was used instead of the Zeiss.

1	Pigment epithelium.
1.pi	The densest pigmented section of the pigment epithelium, just below the nucleus.
2	Rods and cones.
3	Outer nuclear layer.
4	Outer reticular layer.
5	Horizontal cells.
6	Inner nuclear layer.
7	Spongioblastic layer.
8	Inner reticular layer.
9	Ganglionic layer.
10	Optic fiber layer.
am	Ameloid bodies of the pigment epithelium.
cn	cones.
cn.nl	cone nuclei.
chr	choroid.
chr.f	choroidal fissure.
cps	blood corpuscles.
d	dorsal aspect of eye.
hd	hyaloid membrane.
l	left side of eye.
lns	lens.
m	Müllerian nuclei.
msc	eye muscle.
i.1	outer layer of iris.
i.2	inner layer of iris.
nl	nucleus.
nl.l	elongate nuclei of the pars ciliaris.
nl.g	nuclei of the ganglionic cells.
n.op	optic nerve.
ot	otolith.
p	pupil.
pr.nl	processes of the cone nuclei.
r	right side.
rd	rod.
scl	sclera.
scl.c	scleral cartilage.
subo	suborbital.
v	ventral aspect.
x	flattened cells beneath the pigmented layer of doubtful significance.
y	flattened cells beneath the inner nuclear layer of doubtful significance.

Chologaster papilliferus.

Fig. 1. Section through the lower left half of the iris and neighboring structures, seen from in front. *i* iris. *c* cornea. *ep* epidermis. *d* dermis. *sb.o* suborbital bone.

Fig. 2. Section of right half of head passing through eye and showing neighboring parts.

Fig. 3. Section through the retina at the entrance of the optic nerve. *scl* sclera. *ch* choroid. *pg.ch* choroidal pigment.

Fig. 4. Section through lower half of left eye seen from behind. The eye was depigmented. Oval nuclei at ora serrata. *sc* sclera. *ch* choroid. *i* iris. *lg.c* ligamentum ciliare.

Fig. 5. Nuclei of the epithelial layer of the lens of Chologaster.

Fig. 6. Cross section of Chologaster at the optic nerve.

Amblyopsis ct. al.

Fig. 7. Cross section of Amblyopsis at the eye.

Fig. 8*a* and *b*. Two successive sections through the right eye of a very old individual, 130 mm long, showing the lens. 2 mm and 4.

Fig. 9. Outline section of the left eye of an individual 108 mm long showing the most highly developed lens observed. 2 mm and 4.

Fig. 9*a*. Cross section of part of the head of Chologaster agassizii.

Fig. 9*b*. Lower part of iris of Chologaster agassizii, 62 mm long. The pigment is ordinarily much thinner. 2 mm and 4.

Fig. 9*c*. Lower part of iris of Zygonectes notatus. 8 mm and 4.

Fig. 9*d*. Cross section of part of the head of Troglichthys, 25 mm long, showing position and proportions of the eye.

Fig. 9*e*. Head of Troglichthys rosae seen from above showing the relative position of the eyes and the tactile organs. Cleared in Xylol. 35 mm long.

Fig. 9*f*. Part of the same head showing the eyes with their peculiar pigmentation and the distribution of pigment cells in the surrounding tissues.

Fig. 10. Vertical section through the retina of Zygonectes notatus. 2 mm and 6.

Fig. 11. Tangential section of the retina at the depth of the cone bodies showing the relation of the twin cones to the rods. 2 mm and 6.

Figures 12—19 Chologaster papilliferus.

Fig. 12. Section of the inner surface of the retina nearly tangential at the entrance of the optic nerve, showing the distribution of the ganglionic cells and of the optic fiber tracts. 4 mm and 4.

Fig. 13. Vertical section of the pigment cells of a retina depigmented by chromic acid. 2 mm and 4.

Fig. 14. Tangential section through the pigment cells of the same retina. The upper part of the figure passes through the nucleated portion of the cells, the middle through the processes of the cells and the lower through the cones, the pigment cell processes being no longer distinct. 2 mm and 4.

Fig. 15. Vertical section through the retina, depigmented with chromic acid and stained with Biondi-Ehrlich's three colors. 2 mm and 4.

Figures 16—19 a series of four oblique sections through the retina. 2 mm and 4.

Fig. 16 passes from the outer margin of the retina to the base of the cone bodies.

Fig. 17 passes through the basal segments of the cones.

Fig. 18 passes through the cone nuclei.

Fig. 19 passes through the outer limiting membrane, the outer nuclear layer with the cone cell processes, the outer reticular layer and the outermost layer of the outer nuclear layer. The nuclei in the last layer are frequently in pairs, but they do not correspond to and are much less numerous than the twin-cones.

Figures 20—20*a* Chologaster agassizii.

Fig. 20. Vertical section through the retina of an individual 38 mm long.

Fig. 20*a*. Vertical section through the retina of an individual 62 mm long, the rods and cones and pigment layers are omitted.

Figures 21—29 Chologaster cornutus.

Figures 21—25 from a specimen 27 mm long; 26—29 from a specimen 47 mm long.

Fig. 21. Entrance of Optic nerve and part of the retina. 2 mm and 6.

Fig. 22. Oblique section through the pigment layer to near the outer nuclear layer. 2 mm and 4.

Fig. 23. Bases of Cones and the underlying nuclei of the outer layer. The nuclei, in black, are in deeper focus. 2 mm and 8.

Fig. 24. Nuclei of the outer nuclear layer and the deeper lying nuclei of the inner nuclear layer. 2 mm and 8.

Fig. 25. Section tangential to the ganglionic layer showing the distribution of the ganglionic nuclei and on the left a row of nuclei of the innner nuclear layer. 2 mm and 4.

Fig. 26. Section of the retina through an old individual. The pigmented layer is left blank. All the nuclei are as seen in one focus except the vertical Müllerian nucleus which is from another section. 2 mm and 6.

Fig. 27. Fragment of the same retina at another point.

Fig. 28. Cells of the lens epithelium, surface and tangential. 2 mm and 4.

Fig. 29. Cells and blood cells from the hyaloid membrane.

Figures 29—41 Amblyopsis spelæus.

Fig. 30. Section through the eye of an individual 75 mm long killed with Chromic acid and stained with Biondi-Ehrlich's three color mixture. This is the most highly developed eye seen. 2 mm and 4.

Fig. 31. Part of the next section, passing through the iris.

Fig. 32. Horizontal section through the right eye of a specimen 25 mm long from above. A large branch of the optic nerve is seen to pass in front of the cone of ganglionic cells. This is not constant and in the left eye of the same individual the largest strand passes behind the ganglionic central mass. The eye at this stage is noted for the number of ganglionic cells lying in front of the inner reticular layer and the central ganglionic mass.

Figures 33—38 from an individual 35 mm long killed in Perenyi's fluid and stained with Mayer's haemalaun. Figures 33—36 are from the left eye, 37 and 38 from the right eye. All under the lenses 2 mm and 4.

Fig. 33 shows the outer nuclear layer in the center, the choroidal infolding on the left. The lower part of the figure passes through the choroidal fissure area and the pigment cells are here undifferentiated, quite different from those of the dorsal part of the same section.

Fig. 34 is farther forward and shows strands of the optic nerve and the elongated nuclei of the inner layer of the iris irregularly arranged (*nl.l*). Choroid and sclera can not be separated from each other except where the latter is differentiated as cartilage, in front of the eye.

Figs. 35 and 36 are the surface and deeper focus of a section passing through the iris and central ganglionic cells. In figure 36 the irideal structure with the elongated inner nuclei is well shown.

Fig. 37. Passes near the center of the eye. The choroidal fissure epithelium is seen below and an irregular mass of sections through the elongated irideal cells. *nl.l.*

Fig. 38. Passes through the optic nerve and the pupil of the same eye as figure 37.

Figures 39—41 from an individual 95 mm long killed in picric acid and stained with a mixture of haemalaun and indigo carmine. Figures made with Bausch and Lomb $^1/_{12}$ immersion and 4 eye piece.

Fig. 39. Section of the right eye. Choroidal groove with one of the scleral cartilages in front of the eye. The nuclear layers are thinner than usual. The densely pigmented segment of the pigment cells forms a conspicuous layer just below the pigment nuclei.

Fig. 40. The next section after 39 showing a group of elongate uveal cells.

Fig. 41. A section near the posterior face of the left eye of the same individual showing particularly the position of one of the scleral cartilages behind the eye and the thick choroid filled with a more or less angular mass of granular pigment. This eye shows one of the largest accumulations of pigment noticed.

Figures 42—49 Typhlichthys subterraneus.

All ganglionic nuclei with heavy outlines.

Fig. 42. Vertical section through the eye of an individual 25 mm long.

Fig. 43. Iris of the same eye, two sections nearer the center of the eye.

Fig. 44. Vertical sagittal section through the right eye of the same individual. The two eyes belong to the same series of sections and the figures show all the irregular positions of the eyes. Scleral elements shaded, ganglionic nuclei with heavy outlines.

Fig. 45. A group of Müllerian cells from the same individual.

Fig. 46. Vertical section through the left eye of a specimen 40 mm long. The inner layer of cells of the uvea shows well as a series of elongated nuclei. The section, while passing through the ganglionic layer, does not pass through the pupil. A strand of elongated nuclei through the middle of the ganglionic layer represents the hyaloid membrane.

Fig. 47. Left eye, median vertical section of an individual 42 mm long. Showing the iris, lens and hyaloid. 2 mm and 4.

Fig. 48. Section through iris and lens of the right eye of the same individual. 2 mm and 4.

Fig. 49. Horizontal section of the eye of a specimen 40 mm long. $^1/_{12}$ and 4.

Figures 50—56 Troglichthys rosae.

Figs. 50 and 51. Two horizontal sections through the eye showing the extent of the scleral (*scl*) cartilages and the tendons of the oblique and rectus muscles (*msc*). Fig. 50 represents the section just above Fig. 51. From an individual 34 mm long. Drawn under a magnification of 560 diameters.

Figs. 52 and 53. Two cross sections of the eye of a specimen preserved in alcohol and 38 mm long. These sections show the variable extent of the pigment, the choroidal (*ch*) pigment and the scleral cartilages. The extent of the latter is represented by the dotted line in one of the figures. ⨯ 560.

Figs. 54 and 55. Cross sections through the right and left eye of an individual 25 mm long. Both sections pass through the lens. Fig. 54 is a composite from three sections. Fig. 55 represents one section, the lens is seen in the next section which is represented in 55*a*. ⨯ 560.

Fig. 56. Horizontal section through the only eye found with central ganglionic cells. From an individual 34 mm long. ⨯ 560.

Figures 57—61. From photographs of the upper half of the heads cleared in xylol, all under the same magnification.

Fig. 57. Chologaster papilliferus 35 mm long.
Fig. 58. Chologaster agassizii 41 mm long.
Fig. 59. Amblyopsis spelæus 35 mm long.
Fig. 60. Troglichthys rosae 38 mm long.
Fig. 61. Typhlichthys subterraneus about 35 mm long.

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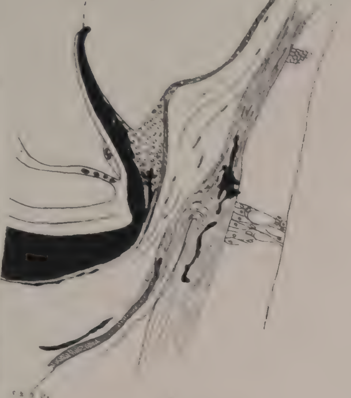

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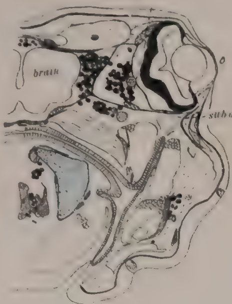

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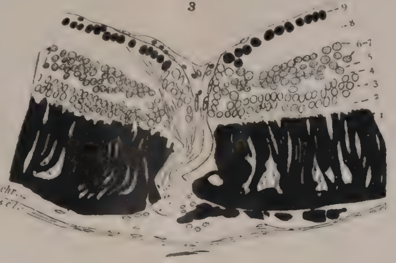

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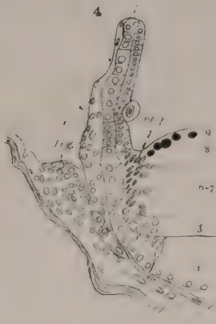

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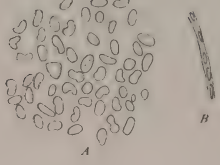

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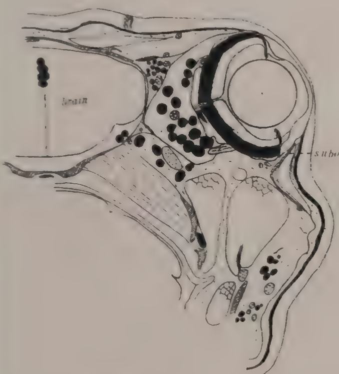

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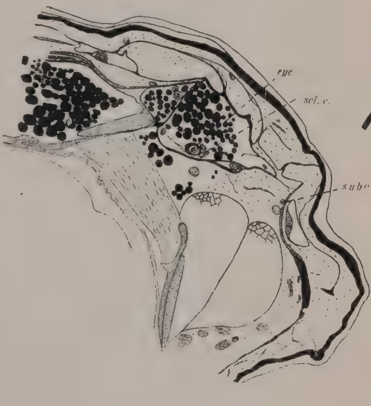

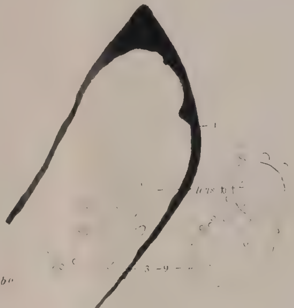

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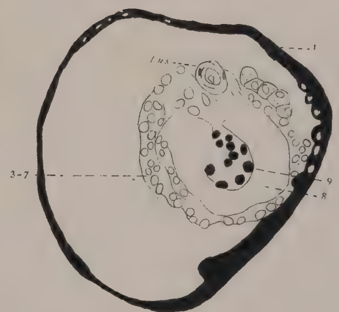

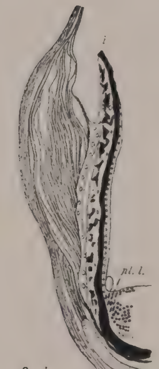

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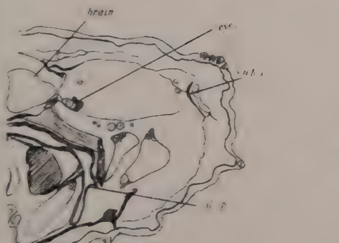

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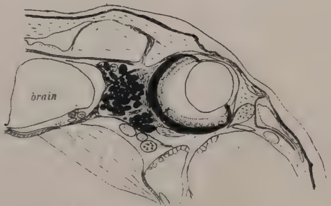

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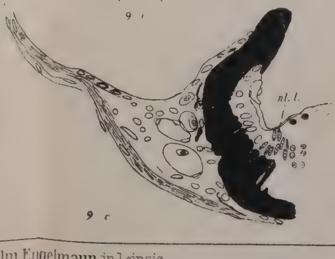

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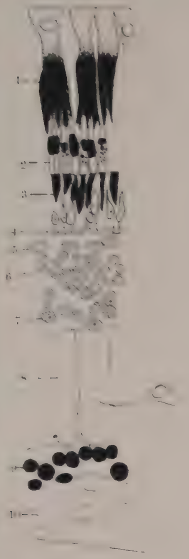

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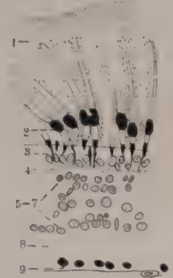

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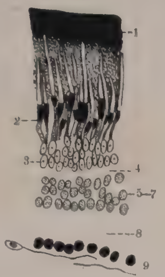

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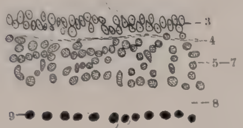

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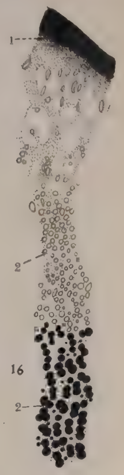

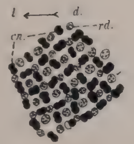

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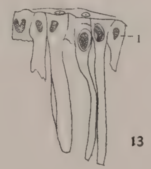

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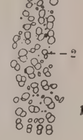

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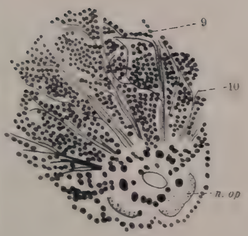

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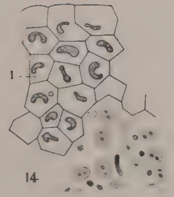

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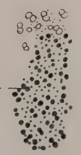

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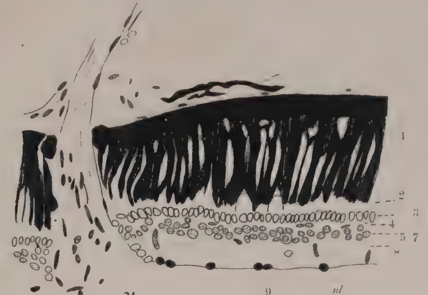

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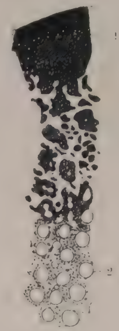

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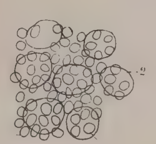

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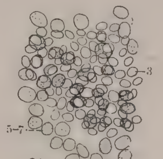

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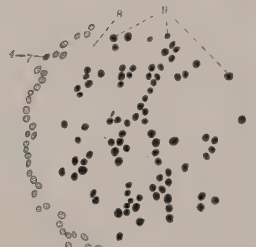

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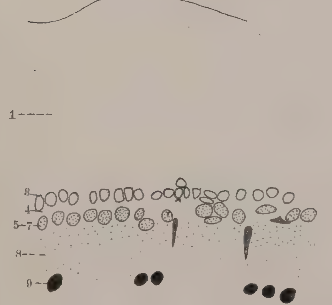

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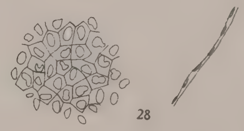

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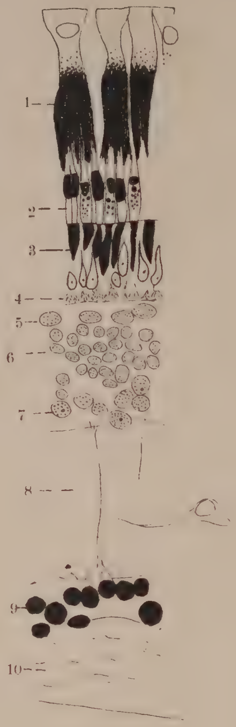
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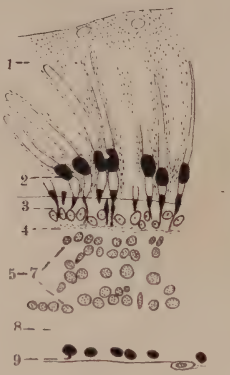
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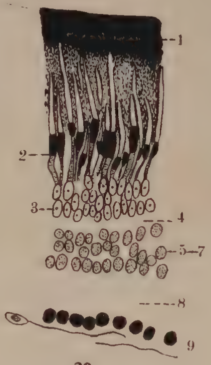
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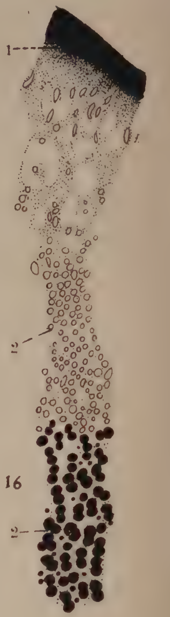
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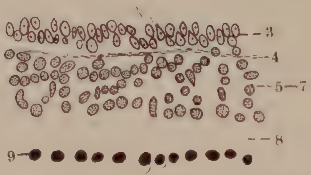
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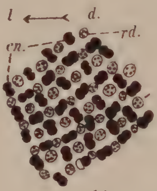
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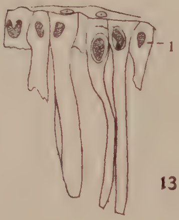
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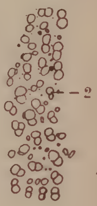
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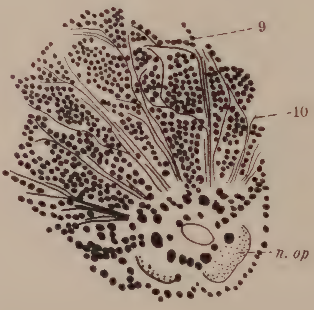
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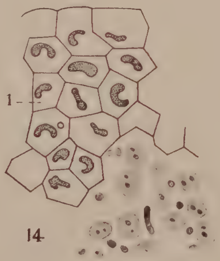
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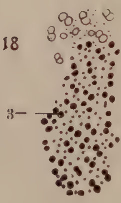
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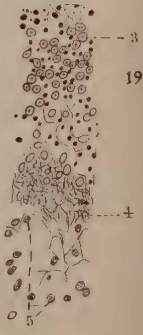
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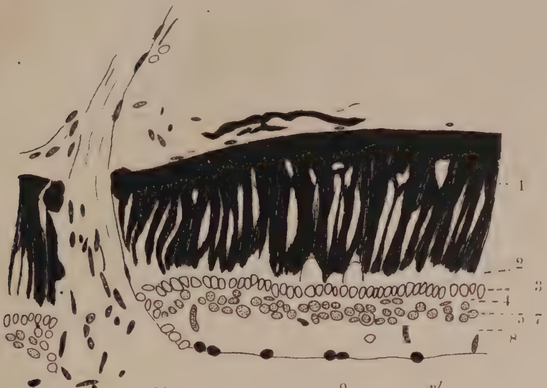

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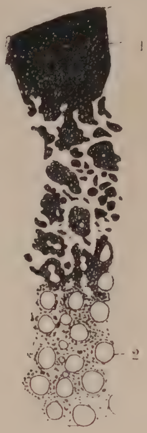

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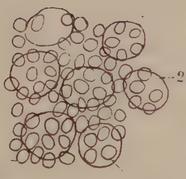

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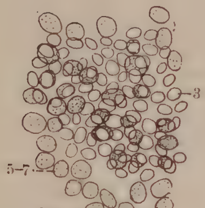

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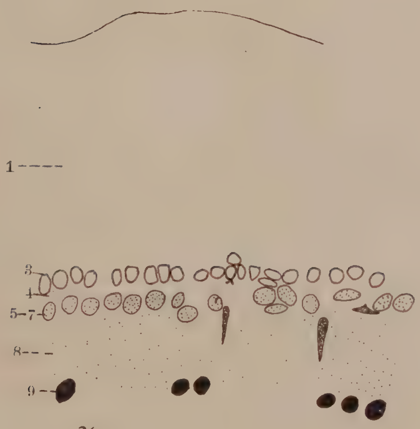

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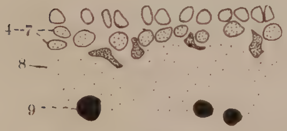

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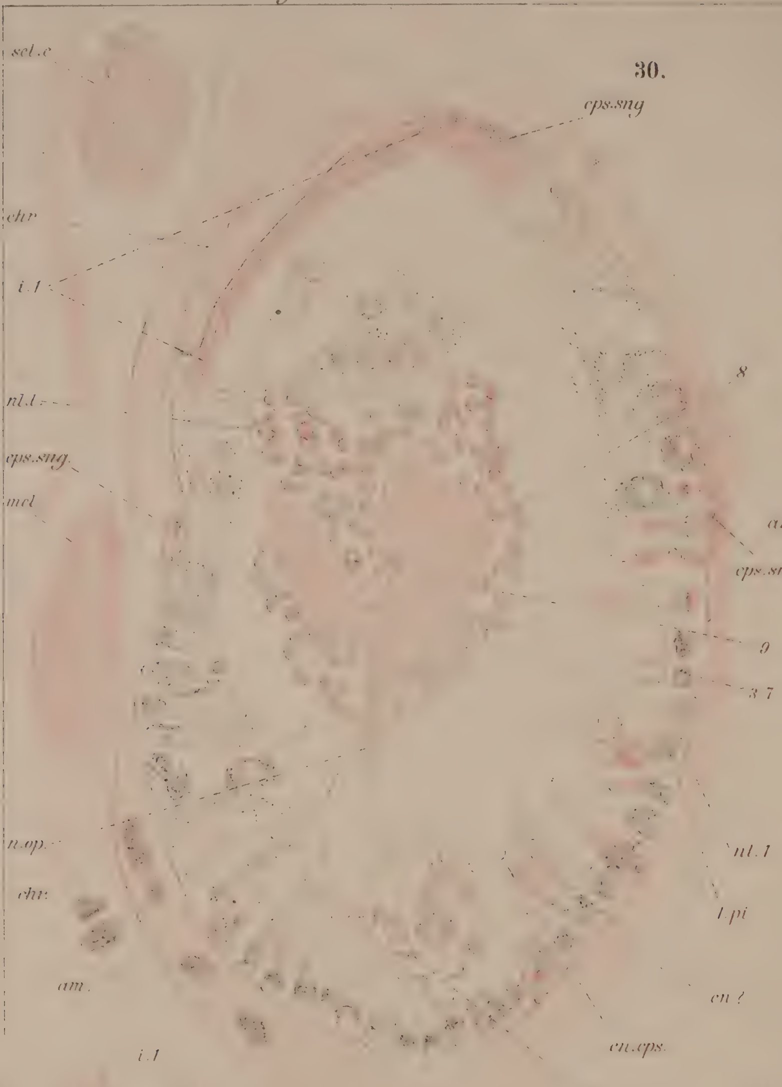

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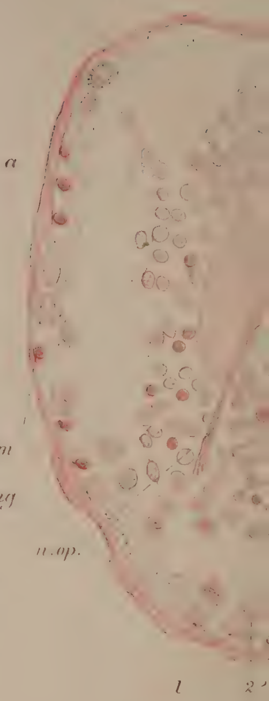

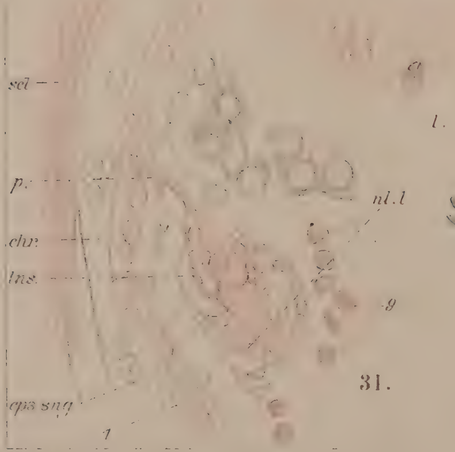

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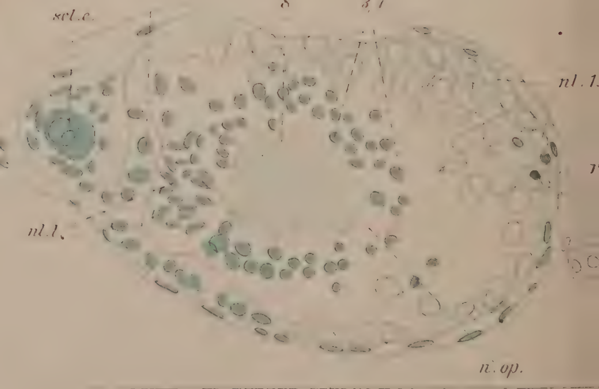

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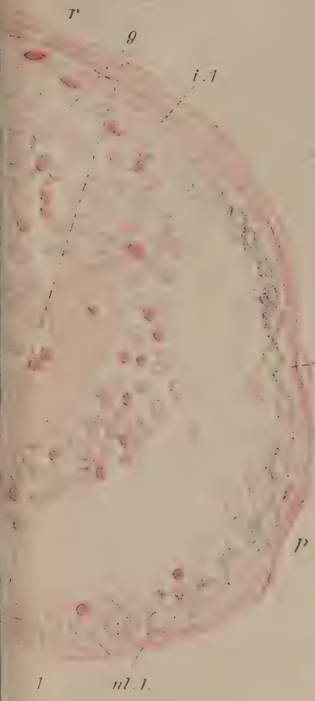

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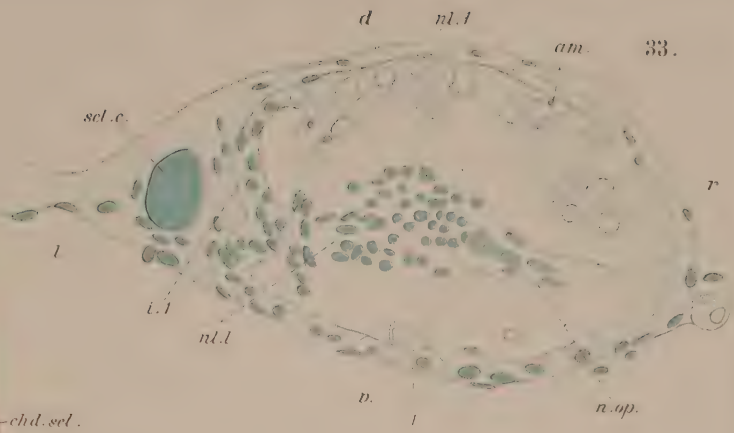

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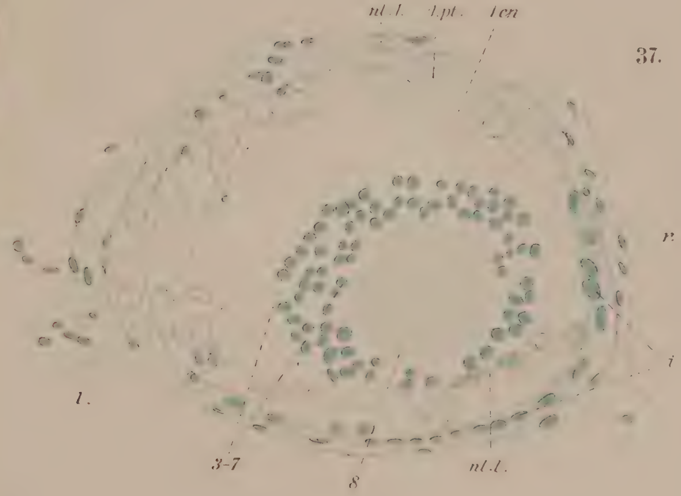

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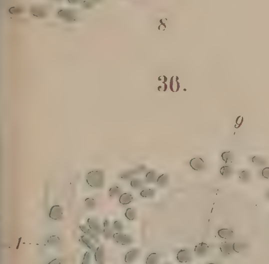

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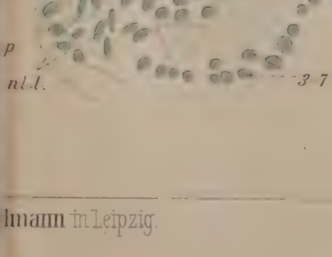

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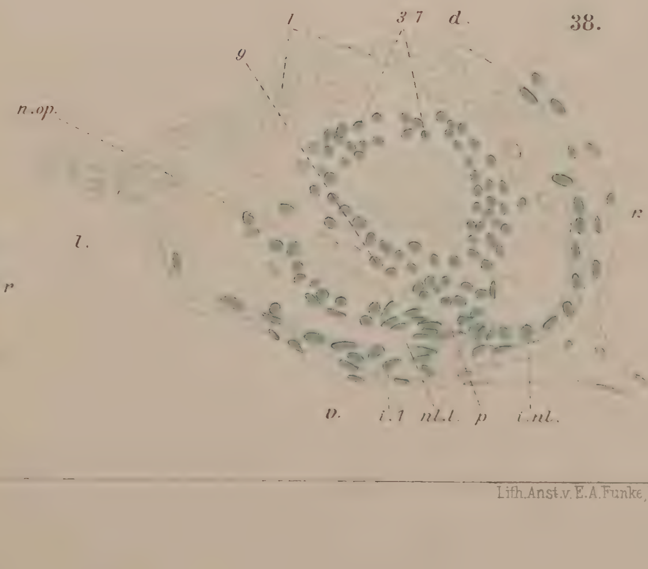

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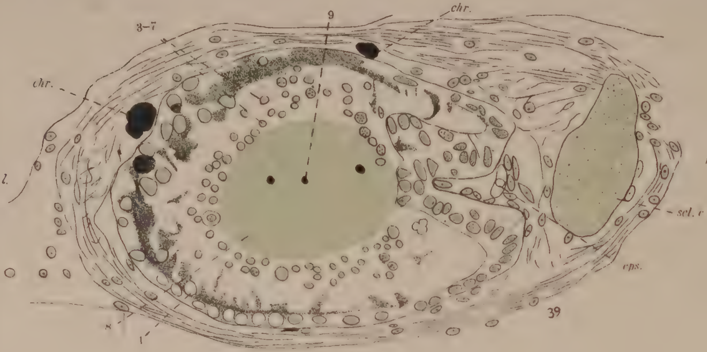

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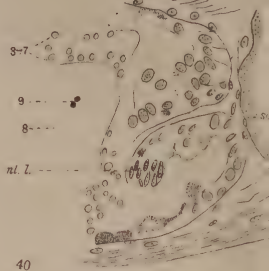

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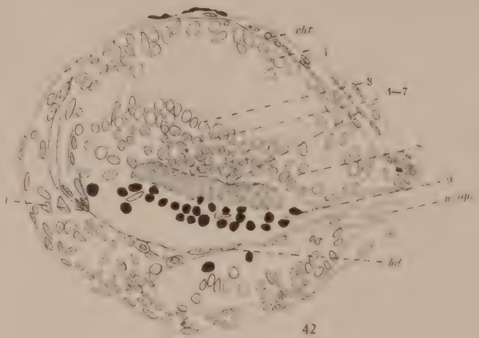

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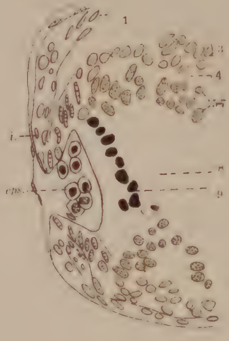

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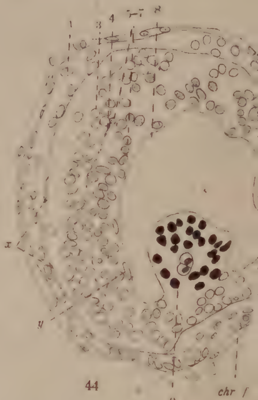

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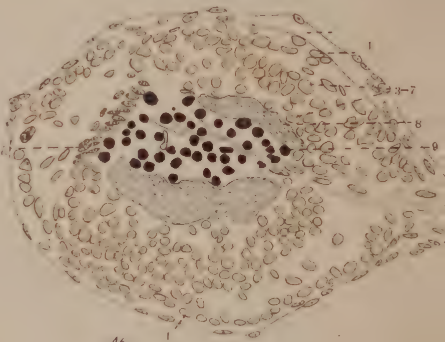

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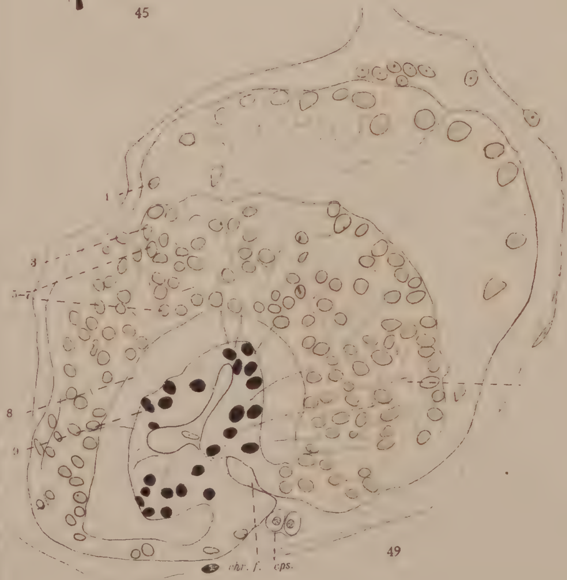

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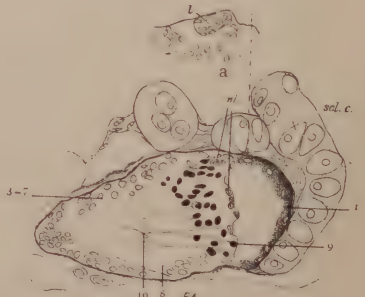

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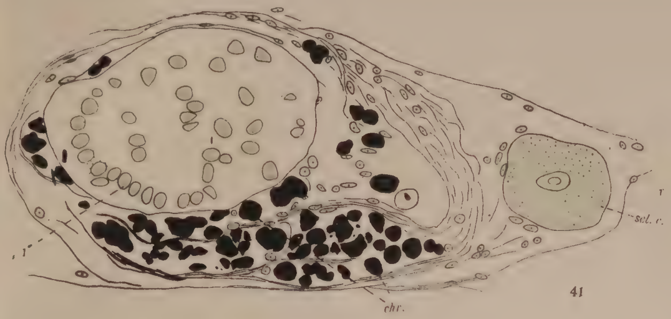

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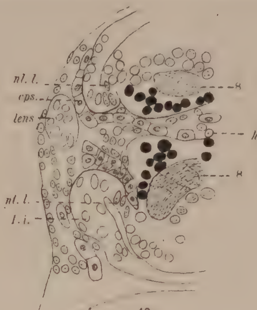

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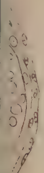

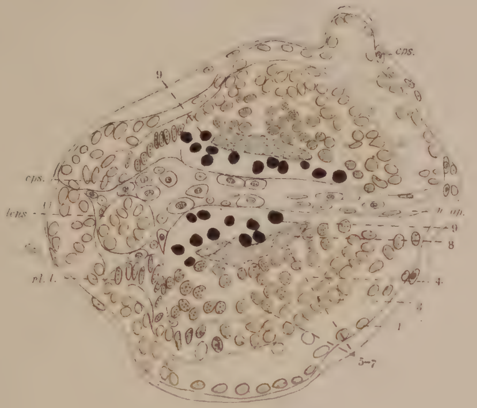

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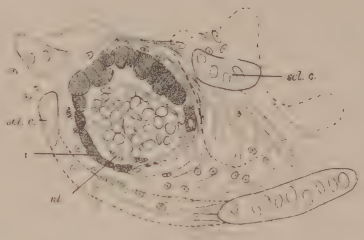

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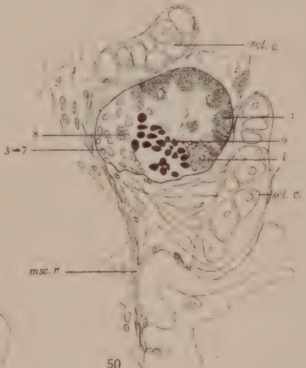

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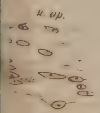

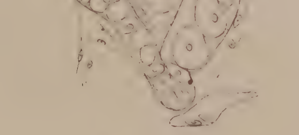

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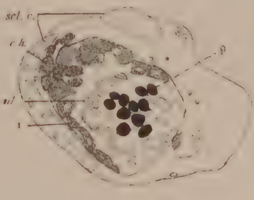

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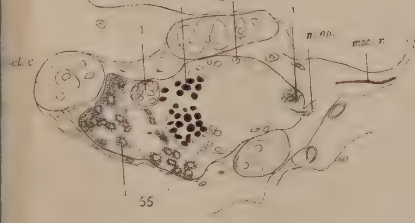

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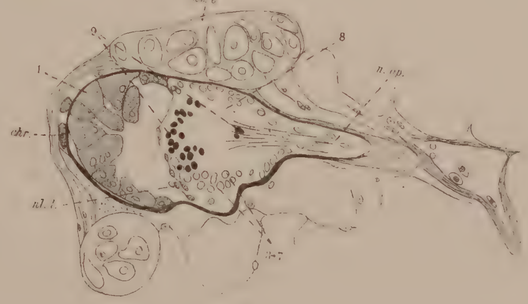

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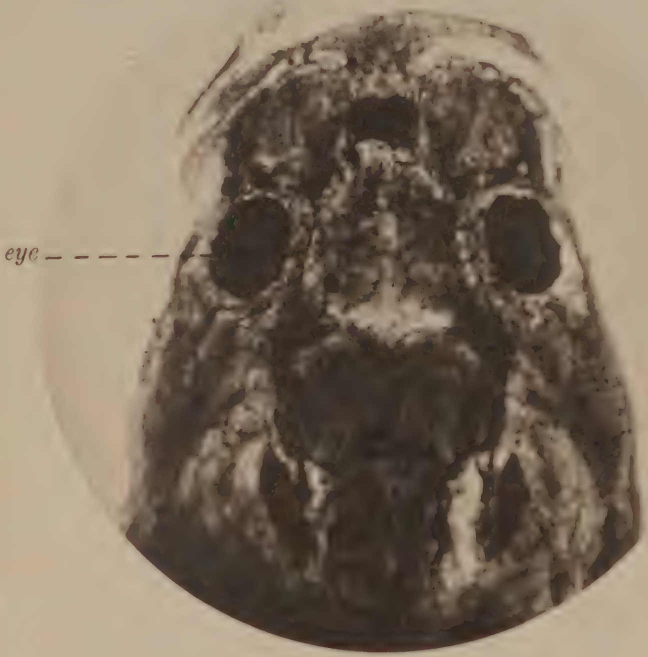

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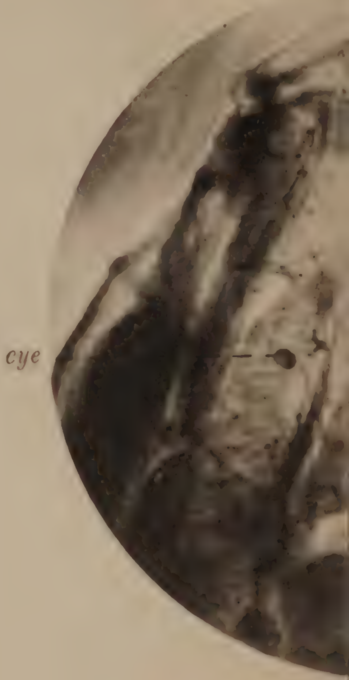

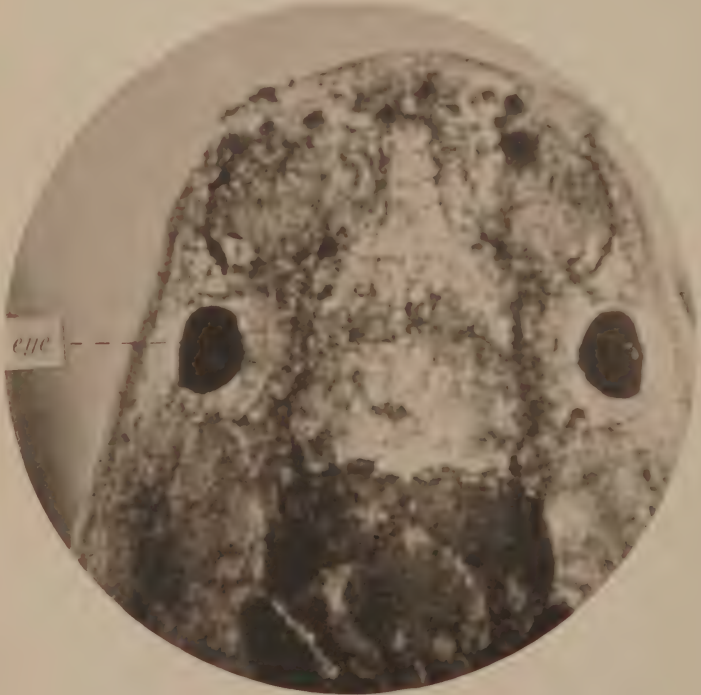

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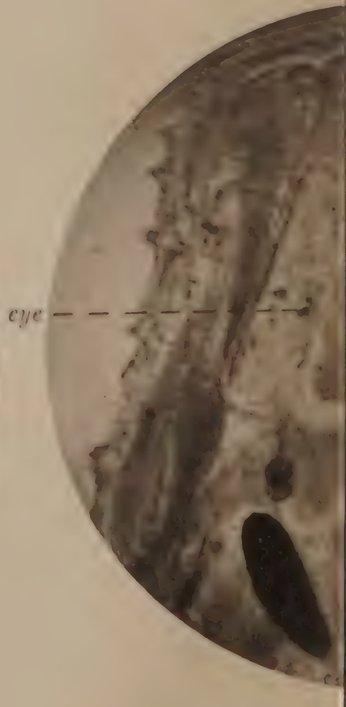

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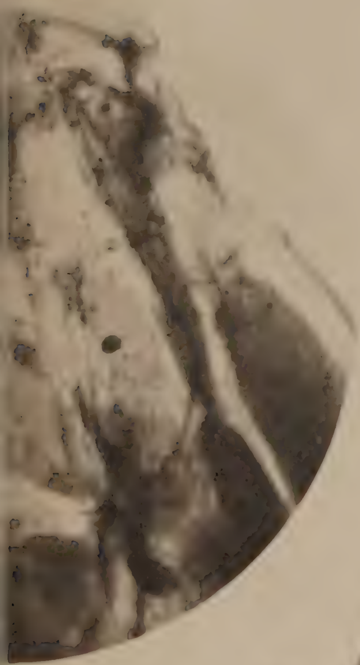

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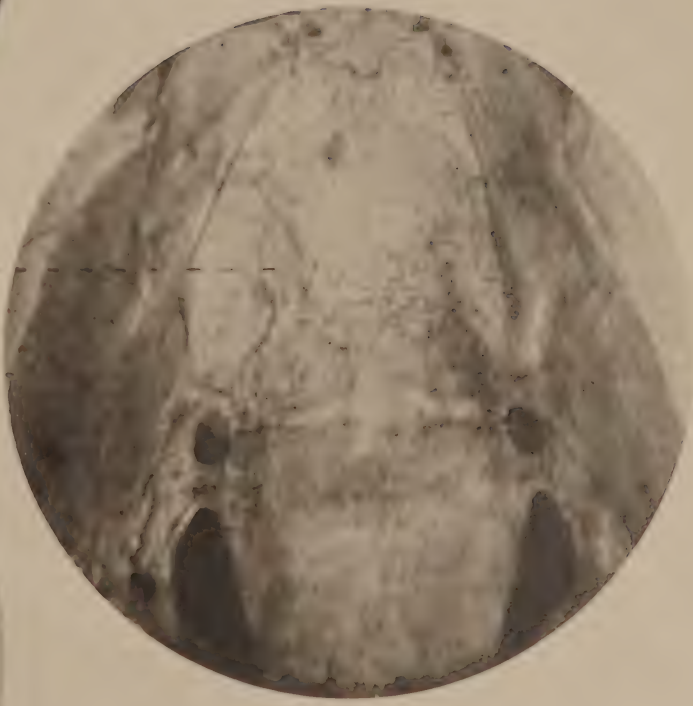

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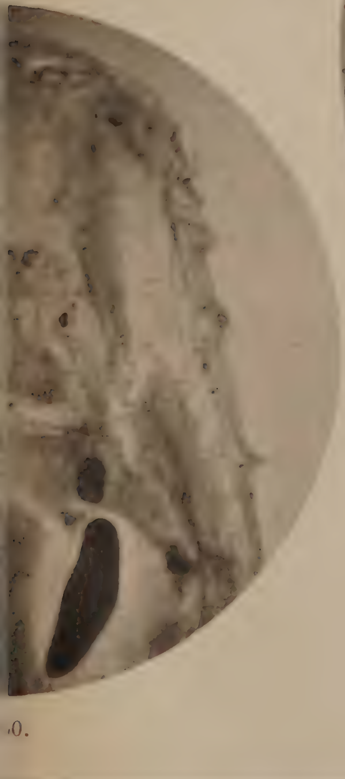

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